



सयमेव जयते

**INDIAN AGRICULTURAL**  
**RESEARCH INSTITUTE, NEW DELHI**

**L.A.R.I. 6**

**GENLK—4/IDIARI/60—16-3-61—5.000**







# University of California Publications in ZOOLOGY

VOLUME XXX

1926-1929

EDITORS

JOSEPH GRINNELL

SAMUEL JACKSON HOLMFS

CHARLES ATWOOD KOFOID

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA  
1930



# CONTENTS

|   | PAGES   |
|---|---------|
| 1. The Pocket Gopher of Honey Lake Valley, by Joseph Grinnell; plate 1 .....  | 1-6     |
| 2. The Muscular Anatomy of Three Mustelid Mammals, <i>Mephitis</i> , <i>Spilogale</i> , and <i>Martes</i> , by E. Raymond Hall; 5 figures in text.....  | 7-38    |
| 3. Systematic Notes on the Subspecies of <i>Bassariscus astutus</i> with Description of One New Form from California, by E. Raymond Hall; plates 2 and 3 .....  | 39-50   |
| 4. Report on a Collection of Birds and Mammals from the Atlin Region, Northern British Columbia, by Harry S. Swarth; plates 4-8; 11 figures in text .....   | 51-162  |
| 5. New Subspecies of Birds ( <i>Penthestes</i> , <i>Baeolophus</i> , <i>Psaltiriparus</i> , <i>Chamaea</i> ) from the Pacific Coast of North America, by Joseph Grinnell and Harry S. Swarth; 2 figures in text ..... | 163-175 |
| 6. A Systematic Study of some Pocket Gophers from Western Nevada, by Joseph Grinnell; plates 9-11 .....   | 177-188 |
| 7. An Outbreak of House Mice in Kern County, California, by E. Raymond Hall .....   | 189-203 |
| 8. The Muscular Anatomy of the American Badger ( <i>Taxidea taxus</i> ), by E. Raymond Hall; 2 figures in text .....  | 205-219 |
| 9. Variation within a Brood of Pacific Garter Snakes, by Edna M. Fisher; 1 figure in text .....   | 221-229 |
| 10. A New Race of Black Bear from Vancouver Island, British Columbia, with Remarks on other Northwest Coast Forms of <i>Euarctos</i> , by E. Raymond Hall; plates 12, 13 .....  | 231-242 |
| 11. Records of Supernumerary Teeth in Bears, by E. Raymond Hall; plates 14, 15; 1 figure in text .....  | 243-250 |
| 12. Variations in the Fox Sparrow ( <i>Passerella iliaca</i> ) with Reference to Natural History and Osteology, by Jean M. Linsdale; plates 16-20, 38 figures in text .....   | 251-392 |
| 13. The Molts of the Loggerhead Shrike, <i>Lanius ludovicianus</i> Linnaeus, by Alden H. Miller; 4 figures in text .....  | 393-417 |
| 14. Mammals Collected by Charles D. Brower at Point Barrow, Alaska, by E. Raymond Hall .....  | 419-425 |
| 15. Pterylography of Certain North American Woodpeckers, by William Henry Burt; 7 figures in text .....   | 427-442 |
| 16. Notes on the Genus <i>Ensatina</i> in California, with Description of a New Species from the Sierra Nevada, by Tracy I. Storer .....  | 443-452 |
| 17. A New Kangaroo Rat from the Upper Sacramento Valley, California, by Joseph Grinnell and Jean M. Linsdale; 1 figure in text .....  | 453-459 |
| Index .....   | 461-467 |



THE POCKET GOPHER OF  
HONEY LAKE VALLEY

BY

. JOSEPH GRINNELL

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 1, pp. 1-6, plate 1

Issued August 18, 1926

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA



CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# THE POCKET GOPHER OF HONEY LAKE VALLEY

BY

JOSEPH GRINNELL

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

Early in October, 1922, Mrs. Hilda Wood Grinnell and the writer did a few days' collecting near the north shore of Honey Lake, Lassen County, California. Our camp was on the Fleming ranch, near Wendel and some six miles air-line northwest of the old station of Amedee. Here, among the several things of special interest, we found in the salt-grass pastures a form of pocket gopher new to us. We were struck by the great size of the mounds made, the largest we had ever seen anywhere. Three of these, fresh ones, were measured and proved to be of 1200, 1140, and 1050 millimeters diameter, and of 140, 180, and 210 mm. greatest depth, respectively. Three burrows opened up proved to have inside diameters of 65, 75, and 75 mm., respectively. These mounds were, it is true, the largest in sight, the rest, scores in number in this pasture which was limited by a slough on one side and a jungle of willows on the other, being more or less smaller; but the average of all seemed conspicuously large.

Naturally, much of the grass was, in the aggregate, buried by the fine-textured soil brought up from below. The sod was heavy, at the surface a dense tangle of the underground stems of the salt-grass (*Distichlis spicata*). Upon these stems the gophers were evidently subsisting almost, if not quite, exclusively. We trapped and prepared for the Museum of Vertebrate Zoology three specimens of the gophers from this place.

On June 5, 1925, Mr. Joseph Dixon of the Museum staff took the trouble, at my suggestion, to stop off at Susanville (Lassen County) on one of his trips afield and trap some gophers there. The main valley tributary to the basin of Honey Lake is that of the Susan River, which stream emerges from a mountain cañon just above the town of Susanville and enters a broad flood-plain which extends thence



to the lake. Mr. Dixon trapped in an alfalfa field two miles south of the town and obtained four gophers, these proving to be of the same species as the ones from our Honey Lake station of capture, 28 miles east-southeast, this species doubtless inhabiting the bottom-lands all the way between. One of Mr. Dixon's gophers is the old male which is selected as the type of the new form now to be described.

### ***Thomomys relictus*, new species**

#### **Honey Lake Pocket Gopher**

*Type*.—Male, old adult, skin and skull; no. 35271, Mus. Vert. Zool.; valley of Susan River two miles south of Susanville, Lassen County, California; June 5, 1925; collected by J. Dixon, orig. no. 8581.

*Characters*.—Size very large (males with total length of 242 to 280 mm., hind foot 35 to 38.6); ears small (4 to 6 mm. from crown); coloration ashy gray; skull heavily built, ridged and angular; rostrum and nasals long; premaxillary tongues narrowly attenuate posteriorly, their ends extending 2 mm. behind posterior ends of nasals; interparietal small and triangular; auditory bullae large, truncate in profile anteriorly as viewed from beneath; teeth large, and incisors far forwardly projecting. (See accompanying table for detailed measurements.)

*Distribution*.—So far as known, restricted to the bed of Honey Lake Valley, Lassen County, California, where common in the borderlands of Honey Lake proper, and thence up the main tributary valley of the Susan River as far as Susanville.

*Relationships*.—I have, of course, made full use, in this connection, of Vernon Bailey's valuable Revision of the Pocket Gophers of the Genus *Thomomys* (N. Am. Fauna, No. 39, 1915). Indeed, without carefully studying the general systematic digest therein available, it would be folly to hazard further new names in this complex group of mammals. Bailey (pp. 73-74) gives the range of his *Thomomys perpallidus canus*, described from the Smoke Creek Desert, Nevada, as extending "west to Honey Lake, Cal."—on the basis of two specimens from California. One of these, a female collected at Amedee (near the east shore of Honey Lake) he comments upon in comparison with typical *canus* as being "still more ashen gray." This specimen thus undoubtedly belonged to the species I now name *relictus*; in other words, the previous ascription of *canus* to California must now be transferred to *relictus*.

Through the courtesy of Dr. E. W. Nelson, Chief of the Bureau of Biological Survey, Washington, D. C., I have before me four topotypes of *Thomomys perpallidus canus*. Compared with these, the Honey Lake Pocket Gopher is in general appearance similar, but is decidedly larger, with coloration slightly grayer. In a partly molted example of *relictus* from six miles northwest of Amedee, date October 4, 1922, the outgoing summer pelage is dusky "pinkish buff" (of Ridgway, 1912), while the incoming new winter pelage is close to light mouse gray. Cranially, the differences between *relictus* and

## MEASUREMENTS (in millimeters) OF THOMOMYS RELICTUS FROM HONEY LAKE VALLEY, LASSEN COUNTY, CALIFORNIA

| No.<br>M.V.Z. | Sex | Age     | Locality                  | Total length | Tail vertebrae | Hind foot | Ear from crown | Weight (in grams) | Basilar length, Hensel | Length nasals | Zygomatic breadth | Mastoid breadth | Width rostrum at middle | Interorbital breadth | Alveolar length, upper molar series |
|---------------|-----|---------|---------------------------|--------------|----------------|-----------|----------------|-------------------|------------------------|---------------|-------------------|-----------------|-------------------------|----------------------|-------------------------------------|
| 35274         | ♀   | young   | 2 miles S Susanville..... | 225          | 62             | 34        | 5              | 134.5             | 34.0                   | 12.9          | .....             | 21.5            | 8.0                     | 7.0                  | 9.4                                 |
| 32992         | ♀   | subad.  | 6 miles NW Amedee.....    | 233          | 76             | 33        | 4              | 162.0             | 37.6                   | 14.8          | 27.3              | 22.8            | 8.8                     | 7.4                  | 9.9                                 |
| 32990         | ♀   | ad.     | 6 miles NW Amedee.....    | 241          | 73             | 31.5      | 4              | 174.5             | 37.4                   | 16.0          | 27.9              | 23.0            | 9.3                     | 6.2                  | 9.8                                 |
| 35273         | ♀   | ad.     | 2 miles S Susanville..... | 255          | 64             | 35        | 6              | 138.0             | 39.6                   | 15.8          | 29.8              | 25.4            | 9.5                     | 7.6                  | 9.3                                 |
| 32991         | ♂   | subad.  | 6 miles NW Amedee.....    | 242          | 75             | 35        | 4              | 193.0             | 38.2                   | 16.1          | 27.9              | 23.1            | 9.3                     | 7.2                  | 9.4                                 |
| 35272         | ♂   | ad.     | 2 miles S Susanville..... | 270          | 78             | 38        | 6              | 158.0             | 40.8                   | 15.7          | 29.2              | 25.4            | 9.6                     | 7.4                  | 9.5                                 |
| 35271         | ♂   | old ad. | 2 miles S Susanville..... | 280          | 80             | 38        | 6              | 325.1             | 45.3                   | 19.4          | 33.3              | 27.8            | 10.5                    | 7.2                  | 9.5                                 |

*canus* are relatively great. Besides being much the larger in mass (sex and age being taken into account), the skull of *relictus* shows longer rostrum, this correlated, maybe, with the far forward-projecting (instead of in-curved) incisor teeth; the nasals are longer, and the paralleling premaxillary tongues are much narrower, more attenuate posteriorly, being but one-half to two-thirds as wide opposite the maxillary mortise in *relictus* as in *canus*; the interparietal is actually smaller, and it is triangular instead of distinctly quadrate. (See pl. 1.)

Now these differences are so great, and the distance between Amedee and Deep Hole so little (scarcely 50 miles air-line), and the chances of commingling of stocks over the intervening territory so remote (because each belongs to a fine-sediment, bottom-land association which is not continuous between, even though the intervening divide altitudinally is low), that I am forced to designate *relictus* as a full species with respect to *canus*. I cannot see, even, that *relictus* belongs to the "*Thomomys perpallidus* group," of Bailey (p. 34), to which *canus* is stated to belong.

In casting about for some other relationship, all the other nearby situated gophers must be ruled out. Upon the range of *relictus* about in different segments of its periphery the ranges of members of the *bottae*, *monticola*, and *fossor* groups; but these are all quite distinct from it. I find just one possibility seemingly worth consideration, and that is with the "*Thomomys townsendii* group," of Bailey; and in superficial appearance (large size and gray coloration) the resemblance of *relictus* to *Thomomys townsendii nevadensis* Merriam is striking. Indeed, I should at once quash the first under the latter, were it not for the cranial differences which I find to obtain. The material at hand representing *nevadensis* is from Big Creek Ranch and Quinn River Crossing, Humboldt County, Nevada (see W. P. Taylor, Univ. Calif. Publ. Zool., vol. 7, 1911, pp. 262-267), and it was included in that which was examined critically by Bailey (pp. 44-45).

The differences in the skull between *relictus* and *nevadensis* are less in number and amount than between *relictus* and *canus*; indeed they comprise only the following, so far as I can see: occipital condyles (in *relictus*) closer together, with notch between (inferior margin of foramen magnum) deeper; brain-case deeper, not so flattened; premaxillary tongues much narrower posteriorly; and incisors slightly more forward-projecting. (See pl. 1.)

In summary, I find four differences between *relictus* and *nevadensis*, six differences between *relictus* and *canus*. The conclusion can be drawn that the real affinities of *relictus* are with the *townsendii* group. Yet I must at once grant the obvious probability of very unequal phylogenetic significance in the different characters designated. As to which of the characters are most likely indicative of descent and which are of more immediately adaptive origin, however, I am unable to say; and I am forced to fall back on that first basis, of relative numbers of characters. By this interpretation, *relictus* is another member in the *townsendii* group; and it is a somewhat differentiated relic, perhaps, from a time and condition when

this group was spread continuously over suitable portions of the northern Great Basin. Now, restriction of appropriate habitat, accompanied by the incursion of other gopher stocks (such as from the *perpallidus* group to the southward), has resulted in the sequestration of the three members of the *townsendii* group as found today.

*Transmitted June 1, 1926.*

## EXPLANATION OF PLATE

### PLATE 1

Dorsal and lateral views of skulls of three species of pocket gophers from northern Nevada and northeastern California. All natural size.

*a*, *Thomomys perpallidus canus*, ♂, no. 78366, U. S. Biol. Surv., Nat. Mus.; Deep Hole, Washoe County, Nevada; May 14, 1896; C. P. Streater.

*b*, *Thomomys relictus*, ♂, no. 35271, Mus. Vert. Zool.; Susanville, Lassen County, California; June 5, 1925; J. Dixon.

*c*, *Thomomys townsendi nevadensis*, ♂, no. 7863, Mus. Vert. Zool.; Quinn River Crossing, Humboldt County, Nevada; June 3, 1909; W. P. Taylor and C. H. Richardson, Jr.

*a*

*b*

*c*



*a*

*b*

*c*



THE MUSCULAR ANATOMY OF THREE  
MUSTELID MAMMALS, MEPHITIS,  
SPILOGALE, AND MARTES

BY

E. RAYMOND HALL



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Vol. 30, No. 2, pp. 7-38, 5 figures in text

Issued September 14, 1926

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# THE MUSCULAR ANATOMY OF THREE MUSTELID MAMMALS, MEPHITIS, SPILOGALE, AND MARTES

BY  
E. RAYMOND HALL

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

## INTRODUCTION

The aim of this paper is to present a description of the musculature of one representative each of the genera *Mephitis*, *Spilogale*, and *Martes*. So far as known no account of the muscular anatomy of any specimen of the genus *Mephitis*, the genus *Spilogale*, or the species *Martes caurina*, has been published. Including the forms dealt with in this paper, the muscular anatomy of only 19 specimens, representing 12 species and 10 genera of the Mustelidae, has been described. Since there are 25 or more Recent genera it seems best not to attempt to classify all these on a basis of their musculature at the present time. It is believed, however, that taxonomic characters of considerable value will be found in the musculature when more forms have been studied. For instance, the failure of any part of the rhomboideus to reach the head in *Mephitis* or *Spilogale*, and the absence of a tenuissimus in *Mephitis*, are points of difference from all other mustelids whose musculature has been described, and are of use systematically in separating the genera. Also the taxonomic value of certain characters, seemingly of family or even ordinal rank, remains to be more accurately determined. For instance, the presence of a fourth head, caput anguli, of the biceps brachii, which among the Carnivora has been found only in the Mustelidae, the presence of the rhomboideus profundus, which outside the Mustelidae has been found only in *Potos flavus*, and the presence of a rhomboideus capitis are three of the several characters listed by Windle and Parsons (1898, pp. 180-182) as diagnostic of all Mustelidae and which at the same time distinguish them from some or all other families of the Carnivora. Now *Mephitis* and *Spilogale* do not possess a rhomboideus capitis; thus the dissection of these two additional genera shows the presence of this muscle not to be constant throughout the family. On the other

hand, the other two of the three above-mentioned characters is constant in the forms here described for the first time.

The identification, pertinent data, and present preservation of the material dissected is as follows:

One specimen of *Mephitis occidentalis*, subsp., no. 2346, collection of Ralph Ellis, Jr.; male adult, skin and complete skeleton; collected in Owens Valley, 5 miles southwest of Lone Pine, Inyo County, California.

One specimen of *Spilogale phenax phenax*, no. 19728, Mus. Vert. Zool.; female adult, skin, skull, and body in alcohol; collected at Gualala, Mendocino County, California.

One specimen of *Martes caurina humboldtensis*, no. 35372, Mus. Vert. Zool.; male adult, skin and complete body skeleton; collected 12 miles northeast of Requa, Del Norte County, California.

The specimen of *Spilogale* consisted of a body from which the head, hyoid apparatus, anal scent glands, and four feet had been removed. The account of muscles found on, or inserting on, these parts of the body, including the muscles of the lower arm and leg, applies only to *Mephitis* and *Martes* unless *Spilogale* is definitely said to be included. Otherwise, the account of any one muscle applies to all three specimens unless individual differences are noted. Description of the skin and facial muscles is reserved for treatment in another connection. The order of arrangement is that employed by Reighard and Jennings (1901) in their account of the anatomy of the cat. The more important papers dealing with the myology of the Mustelidae that have appeared up to the present time are to be found in the bibliography appended to the paper of Windle and Parsons (1898, pp. 184-186).

## MUSCLES OF THE HEAD, HYOID ARCH AND TONGUE

**Digastricus.**—ORIGIN: Paroccipital process and ventral margin of mastoid bone. INSERTION: *Mephitis*, ventral border of mandible on posterior face of abrupt "second angle" which lies directly below  $M_2$ . *Martes*, ventral half of medial face of mandible, anteriorly, from point as far forward as anterior border of  $M_2$  and posteriorly to point slightly behind dental foramen.

**Masseter.**—ORIGIN: Whole of zygomatic arch. INSERTION: Masseteric fossa and lateral surface of angular process of mandible. REMARKS: In both specimens three parts can be distinguished. The

fibers of the superficial part arise from the anterior part of the zygomatic arch and extend back to insert on the angle of the mandible. The second part arises from the posterior third of the zygomatic arch and inserts on the lateral surface of the mandible along the posterior part of the ventral border of the masseteric fossa. Its fibers also extend posteriorly but more ventrally than those of the superficial portion. The third and deepest portion arises from the posterior, ventral, and medial sides of the zygomatic arch and inserts into the masseteric fossa.

**Temporalis.**—**ORIGIN:** In usual manner from temporal fossa. **INSERTION:** Medial side of coronoid process. **REMARKS:** A tendinous sheet is present in both specimens, but no comparison was made of the one in *Martes* with the one in *Mephitis*. In *Mephitis* the muscle fibers of the two parts are fused to the sides of the tendinous sheet; thus the distinctness is less than in some other mustelids, for instance, *Mustela*.

**Pterygoideus.**—**ORIGIN:** Pterygoid fossa and adjacent part of palatine bone. **INSERTION:** Medial surface of angle of mandible and immediately adjacent part of horizontal ramus. **REMARKS:** A tendinous sheet is present between the internal and external parts. The two parts can be separated from one another at their origins but not at their insertions.

**Thyreohyoideus.**—**ORIGIN:** Lateral border of thyroid cartilage. **INSERTION:** Caudal cornu of hyoid.

**Omohyoideus.**—Although carefully looked for in *Spilogale* this muscle was not found. More suitable material for dissection might, however, reveal its presence. **ORIGIN:** Anterior border of scapula at dorsal side of incisura scapulae. **INSERTION:** *Mephitis*, basihyal immediately lateral to sternohyoid. *Martes*, fascia covering laryngeal constrictor muscles. **REMARKS:** This muscle is 2 mm. wide in *Martes* and 2.5 mm. wide in *Mephitis*.

**Geniohyoideus.**—**ORIGIN:** *Mephitis*, mandibular symphysis. *Martes*, ventral half of medial face of mandible from symphysis to point 5 mm. posterior to symphysis. **INSERTION:** Basihyal.

**Stylohyoideus.**—**ORIGIN:** Proximal part of paroccipital process. **INSERTION:** Tympanohyal. **REMARKS:** This muscle is fully five times as large in *Mephitis* as in *Martes*. This is explained by the fact that the paroccipital process and tympanohyal are much farther removed from one another in *Mephitis* than in *Martes*. The superficial part was looked for but not found.

**Mylohyoideus.**—**ORIGIN:** Middle of medial surface of mandible from symphysis to inferior dental foramen. **INSERTION:** Median raphe

which extends from mandibular symphysis to basihyal bone. **REMARKS:** In *Mephitis* some of the posterior fibers are attached to the basihyal.

**Hyoglossus, styloglossus, and genioglossus.**—**ORIGINS:** Dorsal surface of basihyal, stylohyal and mandibular symphysis, respectively. **INSERTION:** Tongue.

## MUSCLES OF THE TRUNK

**Spinotrapezius.**—**ORIGIN:** Neural spines of thoracic vertebrae, as follows: *Mephitis* 4–11, *Spilogale* 3–12, *Martes* 3–9. **INSERTION:** Vertebral end of scapular spine. **REMARKS:** In *Martes* the sheet of fascia common to the two acromiotrapezius muscles extends back over the spinotrapezius. In the other two forms the spinotrapezius is separated, at its origin, from the acromiotrapezius by a gap.

**Acromiotrapezius.**—**ORIGIN:** *Mephitis* and *Spilogale*, anteriorly from mid-dorsal line, posteriorly from tendinous line separating muscles of two sides. *Martes*, the anterior 4 mm. from mid-dorsal line, remainder from broad fascia common to muscles of two sides. **INSERTION:** Spine of scapula. *Mephitis*, between points 10 mm. to 37 mm., in *Spilogale* between points 7 mm. to 21 mm., and in *Martes* between points 10 mm. to 30 mm. distant from vertebral border. **REMARKS:** In *Martes* this muscle is closely associated, on its anterior border, with the clavotrapezius. In *Mephitis*, fibers that arise as the omotrachelian constitute the anterior margin of the acromiotrapezius. In all cases the line of separation between the omotrachelian and the acromiotrapezius is clearly defined, although there is no gap between the two. No part of the muscle takes origin from any neural spine.

**Clavotrapezius.**—**ORIGIN:** *Mephitis*, mid-dorsal line from occiput to point 40 mm. behind same and laterally for distance of 17 mm. on lambdoidal crest. *Spilogale*, as in *Mephitis*, except insertion area extends 20 mm. on mid-dorsal line and 11 mm. laterally on lambdoidal crest. *Martes*, mid-dorsal line from occiput to point 40 mm. behind same, but no part from lambdoidal crest. **INSERTION:** Tendinous line of intersection between clavotrapezius and clavodeltoideus, and a few fibers from rudimentary clavicle except in this specimen of *Mephitis* where no clavicle is present. **REMARKS:** At its origin, in *Mephitis*, this muscle lies against, but is not fused with, the acromiotrapezius; anteriorly it is separated from the sternomastoideus by a distance of 8 mm. In *Spilogale* the clavotrapezius is in contact with both the acromiotrapezius and sternomastoideus and is fused with the former for 6 mm. back from the origin. In *Martes* the three muscles form

one continuous sheet, the acromiotrapezius and clavotrapezius being fused from the point where the omotrachelian passes beneath the latter to the point of origin and the superficial portion of the sternomastoideus is fused with the clavotrapezius from the clavicle to the point of origin.

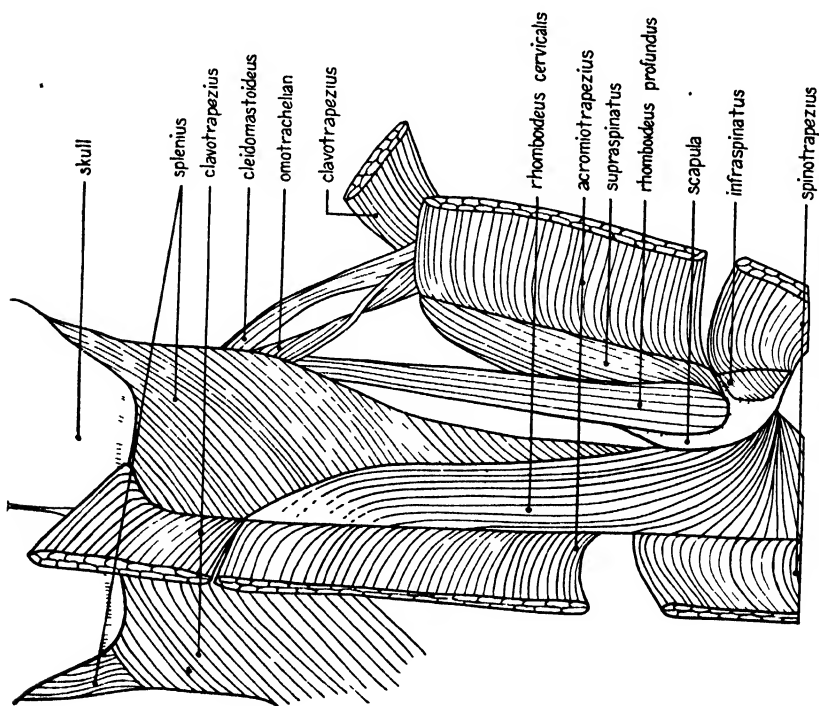
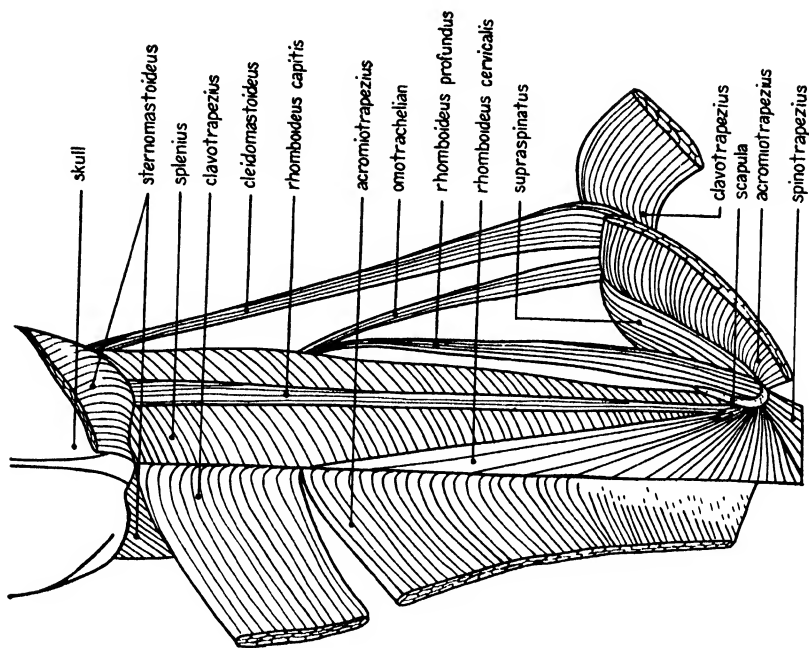
**Rhomboideus cervicalis and capitis.**—**ORIGIN:** *Mephitis*, spines of first 6 thoracic vertebrae and mid-dorsal line of cervical region as far anteriorly as spine of axis, and by fascia that extends over splenius as far as third cervical vertebra. *Spilogale*, the same except that anteriormost fibers take origin directly from mid-dorsal line and farther anteriorly, coming from as far as the first cervical vertebra but not from the head. *Martes*, anteriormost fibers separated as rhomboideus capitis which takes origin from middle of lambdoidal crest and is 7 mm. wide at this place. Cervical portion in *Martes* arises from spines of first 2 thoracic vertebrae and mid-dorsal line of cervical region, anteriorly, as far as axis. **INSERTION:** Vertebral border of scapula from anteriormost extension of triangular surface at end of spine, posteriorly, to within 2 mm. of inferior angle and in *Martes* entirely to inferior angle. **REMARKS:** *Mephitis* and *Spilogale* are unique among the mustelids whose muscular anatomy has so far been examined in that they possess no rhomboideus capitis. At its insertion, in *Martes*, the rhomboideus cervicalis overlaps the serratus posterior. In *Spilogale* the two meet. In *Mephitis*, the posterior 4 mm. of the rhomboideus cervicalis is separated from the remainder and at its insertion is continuous with the serratus posterior.

**Rhomboideus profundus.**—**ORIGIN:** Ventral side of transverse process of atlas. **INSERTION:** By flat tendon into root of scapular spine. **REMARKS:** In all cases this is innervated by a cervical nerve. At the insertion the fibers are distinct from, in fact are not in contact with, those of the remainder of the rhomboideus.

**Cleidomastoideus.**—**ORIGIN:** Tendinous intersection between clavotrapezius and clavobrachialis. Also in *Martes* a few fibers from clavicle. **INSERTION:** *Mephitis*, mastoid bone and paroccipital process. *Martes*, by round tendon on mastoid bone only.

**Omotrachelian (levator claviculae, levator scapulae ventralis).**—**ORIGIN:** Ventral face of transverse process of atlas. **INSERTION:** Metacromion process of scapula. **REMARKS:** At its insertion, the muscle is fused on its dorsal border with the acromiotrapezius.

**Latissimus dorsi.**—**ORIGIN:** *Mephitis*, tips of neural spines of 6th to 11th thoracic vertebrae directly by muscle fibers and behind 11th thoracic by tendinous fascia which extends back to 4th lumbar and by fibers directly from 12th, 13th, and 14th ribs. *Spilogale*, as in *Mephitis*, except that fibers also take origin from 15th rib. *Martes*,

Fig. 1. *Mephitis occidentalis*, X 1.Fig. 2. *Martes caurina*, X 1.

from neural spines of 4th to 10th thoracic vertebrae inclusive, fascia that extends back over lumbar region and from 11th and 12th ribs. INSERTION: In two parts. Ventral fibers converging and inserting with part *C* of pectoralis on antero-internal face of humerus. The dorsal fibers converge and insert with the teres major.

**Levator anguli scapulae** and **serratus magnus**.—ORIGIN: *Mephitis*, transverse processes of last 6 cervical vertebrae, rib cartilages of first 6 ribs, and external surfaces of 7th and 8th ribs. *Spilogale*, transverse processes of last 5 cervical vertebrae, first 6 rib cartilages, and 7th and 8th ribs proper. *Martes*, transverse processes of last 5 cervical vertebrae, first 5 rib cartilages, and external surfaces of 6th and 7th ribs. INSERTION: Ventral border of scapula and vertebral margin of sub-scapular fossa.

**Longissimus dorsi**.—A lateral part, lying just medial to the iliocostalis, separates from the medial portion at the 7th rib in *Mephitis* and *Martes* and the 5th rib in *Spilogale*. In *Mephitis* this mass extends forward to the transverse process of the atlas. Some of the fibers take origin from the transverse processes of the cervical vertebrae. In each of the specimens the origin of fibers on any one given rib is always above the insertion of fibers on that rib. In *Spilogale* fibers extend forward as far as, and insert by tendon on, the transverse process of the 3d cervical vertebra. Other muscle bundles, more dorsal, form a distinct group which takes origin from the transverse processes of the 5th to 3d cervical vertebrae and inserts on the transverse process of the atlas. This group has been distinguished as the longus atlantis. It can also be clearly separated from the remainder of the lateral portion of the longissimus dorsi in *Martes*, but not in *Mephitis*. In *Martes* a separation can also be made between the lateral portion of the longissimus dorsi that inserts on the ribs, and the part that inserts on the cervical vertebrae back to the 7th. This latter portion takes origin from the first to sixth ribs.

**Longus capitis**.—ORIGIN: Transverse process of cervical vertebrae, 2-5. INSERTION: Ventral face of basioecipital.

**Iliocostalis**.—ORIGIN: From ribs; *Mephitis* 14-4, *Spilogale* and *Martes* 12-3. INSERTION: By tendons on ribs; *Mephitis* 10-1, *Spilogale* and *Martes* 9-1. REMARKS: The muscle is confined to the thoracic region. The origins are above the insertions. The muscle is connected with the longissimus dorsi by a small bundle of fibers. The fibers insert on the second to fourth ribs anteriorly from the one on which they take origin.

**Spinalis dorsi**.—This is the medial mass of muscle on the dorsal surface of the back that extends forward and connects the neural spines of the thoracic vertebrae. It becomes differentiated from the



longissimus dorsi at the 8th rib in *Mephitis*, 12th rib in *Spilogale*, and 7th rib in *Martes*. It extends forward, in *Mephitis* to the 2d thoracic, in *Spilogale* to the 7th cervical, and in *Martes* to the 6th cervical.

**Interspinales and intertransversarii.**—These muscles have the usual arrangement, that is, the fibers passing over at least one vertebra between their origin and insertion.

**Splenius.**—ORIGINS: *Mephitis*, entire cervical ligament, neural spines of first 3 cervical vertebrae by muscle fibers, and by fascia that extends posteriorly over underlying muscles. The posteriormost fibers that insert by fascia extend back as far as the 4th thoracic vertebra. *Spilogale*, as in *Mephitis* except that origin is entirely by fibers and as far back as 6th thoracic. *Martes*, as in *Mephitis* except that relatively fewer fibers take origin from fascia that extends posteriorly over deeper muscles. INSERTION: By thin tendon that inserts on whole of lambdoidal crest. Muscle heaviest at lateroventral margin.

**Longissimus capitis.**—Differentiated only in *Martes*. ORIGIN: Articular processes of last 3 cervical vertebrae. INSERTION: By round tendon on mastoid.

**Biventer cervicis.**—Not separable from complexus in *Martes*. ORIGIN: Thoracic vertebrae. *Mephitis* 6–4, *Spilogale* 5–4. INSERTION: Approximately medial fourth of lambdoidal crest.

**Complexus.**—ORIGIN: Articular processes of thoracic and cervical vertebrae. *Mephitis*, 3d cervical to 3d thoracic; *Spilogale*, 4th cervical to 2d thoracic; *Martes*, including biventer cervicis, 5th cervical to 5th thoracic. REMARKS: Only in *Spilogale* is there a gap between the origins of the biventer cervicis and complexus.

**Rectus capitis posterior major.**—ORIGIN: Caudal half of spinous process of axis. INSERTION: On occiput immediately ventral to insertion of complexus and biventer cervicis.

**Rectus capitis posterior medius.**—ORIGIN: Anterior portion of spine of axis. INSERTION: Occiput, medial and ventral to insertion of rectus capitis major. REMARKS: The area of origin includes fully one-half of the lateral face of the spine of the axis in *Mephitis* but scarcely one-fourth of the same in *Martes*.

**Rectus capitis posterior minor.**—ORIGIN: Anterior border of apex of dorsal arch of atlas. INSERTION: Transversely elongated area on occiput above foramen magnum.

**Obliquus inferior.**—ORIGIN: Lateral face of spine of axis. INSERTION: Posterodorsal face of transverse process of atlas.

**Obliquus capitis superior.**—ORIGIN: Anteroventral border of transverse process of atlas. INSERTION: Mastoid bone and line parallel to and ventral to lambdoidal crest. The line extends medially over half the distance from the mastoid bone to the sagittal crest.

**Extensor caudae medialis.**—ORIGIN: Sacral vertebrae. INSERTION: By tendon on dorsal surface of tail vertebrae. REMARKS: This is a continuation of the multifidus spinae.

**Extensor caudae lateralis.**—ORIGIN: Articular processes of anterior caudal and most of lumbar vertebrae. INSERTION: By tendons on dorsal surface of caudal vertebrae. REMARKS: This might be considered as a posterior continuation of the logissimus dorsi.

**Adductor caudae externus.**—ORIGIN: Medial surface of ilium anterior and dorsal to sacrum. INSERTION: Transverse processes and lateral faces of caudal vertebrae. REMARKS: The muscle is actually as large in *Spilogale* as in *Martes* and is about ten times as large in *Mephitis* as in *Martes*.

**Adductor caudae internus.**—ORIGIN: Medial face of pubis and ischium, anterior and slightly ventral to obturator foramen. INSERTION: Transverse processes of caudal vertebrae. *Mephitis* 2-4, *Spilogale* 2-3, *Martes* 1-3.

**Iliocaudalis.**—ORIGIN: Ventral half of medial face of ilium, midway between obturator foramen and sacrum. INSERTION: Ventral surface of caudal vertebrae lateral to flexor caudae brevis. *Mephitis* 2-5, *Spilogale* 2-4, *Martes* 3d.

**Flexor caudae longus.**—ORIGIN: Ventral face of sacrum. INSERTION: lower face of caudal vertebrae.

**Flexor caudae brevis.**—ORIGIN: *Mephitis*, ventral face of sacrum. *Spilogale*, not determined. *Martes*, ventral face of first caudal. INSERTION: Ventral face of caudal vertebrae. REMARKS: Each of the tail muscles is much heavier in *Mephitis* than in *Martes*, a condition correlated, perhaps, with the use of the tail in *Mephitis* as a "warning flag."

**Iliopsoas.**—The muscle mass comprising the quadratus lumborum and psoas major portion of the iliopsoas has the following ORIGIN: Ventral surfaces of lumbar vertebrae and their transverse processes, and in *Mephitis* ventral surfaces of last 4, and in *Spilogale* and *Martes* ventral surfaces of last 3, thoracic vertebrae. The ilial portion from the ventral border of the ilium. INSERTION: Lesser trochanter of femur.

**Quadratus lumborum.**—Its forward extension mentioned in connection with iliopsoas. Posteriorly some fibers insert on the ilium.

**Psoas minor.**—ORIGIN: With general muscle mass composed of quadratus lumborum and psoas major. INSERTION: By long thin tendon on ventral border of ilium slightly in front of acetabulum. REMARKS: At its insertion this muscle is distinct from any other. The separation from the psoas major and quadratus lumborum is greatest

in *Martes*. In *Martes*, where the preservation was best, the origin was definitely determined to be from the last 3 thoracic and first 4 lumbar vertebrae.

**Sternomastoideus.**—**ORIGIN:** Cephalic end of manubrium in front of first costal tubercle. **INSERTION and REMARKS:** In *Mephitis* a heavy, single muscle on either side, not fused with its opposite, inserting by tendon on the mastoid process. Separate from the clavotrapezius at insertion. In *Spilogale* a double muscle, on each side consisting of a lateral thin portion which arises posteriorly on the cranial end of the manubrium, and a thick, heavy, medial portion much like the single muscle in *Mephitis*, arising from the anteriormost part of the manubrium. The thick, heavy, medial portion is not fused with its opposite. It inserts, apparently, as in *Mephitis*. The lateral, thin portion is separate from the medial, heavy portion throughout the entire length, but inserts on the lambdoidal crest between the clavotrapezius and medial portion of the sternomastoid. In *Martes*, on each side, the muscle consists of a superficial, and a deep part. The superficial band is 3 mm. wide at its origin and 18 mm. wide at its insertion. The insertion is by a thin tendon on the lambdoidal crest from a point 6 mm. distant from the sagittal crest to the lower limit of the mastoid process. Although not fused with its opposite, each superficial band is fused with the clavotrapezius from a point 17 mm. distant from the origin of the former to the insertion. The dorsal, deep portion is fused with its opposite for a distance of 30 mm., nearly half of the length of the entire muscle, anteriorly from the point of origin. This deep portion is a round bundle of fibers which inserts by tendon on the mastoid process.

**Sternohyoideus.**—**ORIGIN:** In common with sternothyroideus from dorsal surface of manubrium sterni. **INSERTION:** Basihyal cartilage. **REMARKS:** This muscle was destroyed in *Spilogale*. In the other two specimens it was 3.5 mm. wide. At its insertion a space remains on the basihyal between the two areas of insertion equal to the width of one muscle. The two muscles are not fused.

**Sternothyroideus.**—**ORIGIN:** In common with sternohyoideus from dorsal face of manubrium sterni. **INSERTION:** Lateral face of posterior border of thyroid cartilage. **REMARKS:** In *Martes* the sternothyroideus of each side divides at a point midway up the neck. The medial part inserts as described above. The lateral part, entirely distinct, passes ventral to the medial part and inserts immediately above the sternohyoideus on the basihyal.

**Scalenus longus.**—**ORIGIN:** Transverse processes of cervical vertebrae (see remarks). **INSERTION:** In 3 parts except in *Spilogale*. *A.* On first rib just below its head. Absent only in *Spilogale*. *B.* Ribs

3-4 in *Mephitis* and *Spilogale* and 4 in *Martes*. C. Ribs 7-8 in *Mephitis* and *Martes* and 5-7 in *Spilogale*. REMARKS: In *Mephitis* fibers that take origin from the transverse process of the atlas insert on the first rib. In *Spilogale* and *Martes*, however, the fibers that arise on the transverse process of the atlas do not reach the ribs but insert on the transverse processes of the following 6 cervical vertebrae. Thus it may be correct to say that in *Mephitis* only, does the scalenus take origin from the first cervical.

**Scalenus brevis.**—ORIGIN: Transverse processes of last 3 cervical vertebrae in *Mephitis* and *Spilogale* and last 4 in *Martes*. INSERTION: Ventral half of first rib. REMARKS: In *Mephitis* this muscle is clearly separate from part A of the scalenus longus at the insertion. In *Spilogale* part A of the scalenus longus is not present. In *Martes*, fibers insert from the head to the base of the first rib and are not separable into part A of scalenus longus and scalenus brevis. Perhaps it is not justifiable to separate the scalenus into definite portions in the Mustelidae. The brachial plexus lies ventral to all of the scalenus muscles.

**Rectus capitis anterior.**—ORIGIN: Ventral face of inferior arch of atlas. INSERTION: Posterior portion of basioccipital near postero-internal angle of tympanic bulla.

**Rectus capitis lateralis.**—ORIGIN: Ventral face of transverse process of atlas. INSERTION: Immediately lateral to occipital condyle.

**Longus colli.**—This muscle extends along the ventral side of the vertebral column from the atlas to the 5th thoracic vertebra in *Mephitis* and *Spilogale* and to the 6th in *Martes*.

**Pectoralis.**—Four clearly defined parts are present in each of the three specimens. The origin includes the whole of the sternum from the manubrium to the xiphisternum but does not extend behind the latter. The muscles were slightly damaged in *Spilogale* and are therefore not described in detail. However, they were sufficiently well preserved to show that they are essentially as in *Mephitis*. The parts may be designated by letters. Part A. *Mephitis*, arises from anterior one-seventh of sternum and inserts into pectoral ridge in middle one-fifth of humerus just medial to insertion of clavobrachialis. The fibers extend transversely. In *Martes*, fibers arise from the anterior one-tenth of the sternum. Part B. Deep to A but arising from entire longitudinal extent of sternum except cranial end of manubrium anterior to first costal tubercle. Inserts on pectoral ridge in middle three-elevenths of humerus. At its insertion it is mesial to A, extends slightly farther proximally on humerus, and is divisible into two parts, the anterior of which is less than one-third the mass of the posterior.

In *Martes*, origin anteriorly the same, but posteriorly, extending slightly less than halfway back on sternum. Insertion is broader and more proximal on humerus. More exactly, in *Martes*, the area of insertion is 25 mm. long and terminates at a point 15 mm. distant from the proximal end of the humerus and at a point 20 mm. distant from the distal end of the humerus. Part *C*. Deep to *B*, arising from middle three-fifths of sternum. Inserted into capsule of shoulder and proximal half of humerus. Divisible into two parts at insertion. Fibers of posterior part insert in common with those of cutaneous maximus and latissimus dorsi. In *Martes* arises from slightly more than posterior half of sternum and inserts in common with last two muscles mentioned. A deeper, anterior portion inserts into the capsule of the shoulder joint. The two portions are separated from one another by a distance of 10 mm. at their insertion, and the separation can easily be traced more than four-fifths of the length of the two muscles toward the origin. Part *D*. A small round muscle, entirely distinct from remainder of pectoral mass, arises deep to *A* from cephalic end of manubrium anterior to first costal tubercle and inserts just below greater tuberosity on line with, and immediately anterior to, *B*.

**Serratus posterior superior.**—ORIGIN: Ribs, *Mephitis* 5–10, *Spilogale* 2–10, *Martes* 4–10. INSERTION: Fascia covering longissimus dorsi. REMARKS: The fibers extend dorsally and anteriorly. The slips unite to form one muscle. In *Spilogale* the slip taking origin from the second rib is separate, but inserts in the same manner as the remainder.

**Serratus posterior inferior.**—ORIGIN: *Mephitis*, last 5 ribs. *Spilogale* and *Martes*, last 4 ribs. INSERTION: Fascia covering longissimus dorsi. REMARKS: The parts from the several ribs unite to form one sheet and are removed from the serratus posterior superior by the distance between one rib and the succeeding rib. The fibers extend almost straight inward, or medially, rather than anteriorly as do the fibers of the serratus posterior superior.

**Transversus costarum.**—ORIGIN: By tendinous sheet, between ribs 4–6 in *Mephitis* and 3–4 in *Spilogale* and *Martes*, that covers rectus abdominis and extends to sternum. INSERTION: By fleshy fibers on first rib and its costal cartilage.

**Levatores costarum.**—Each of the muscles takes origin from the transverse process of one vertebra and inserts on the angle of the succeeding rib. They are present on the false as well as true ribs.

**Intercostales externi.**—These muscles are composed of fibers that extend between, and are attached to, the adjacent borders of each two ribs. The fibers extend from their cranial ends caudoventrally. They are lacking between the costal cartilages of the first 9 ribs and in these 8 interspaces the intercostales interni are exposed.

**Intercostales interni.**—These bear the same relation to the ribs as the intercostales externi but lie internal to the latter, and the fibers of the two muscles run at nearly right angles to one another.

**Transverse thoracicus.**—This is the thoracic portion of, and a continuation of, the transversus abdominis. It consists of 7 bands in *Mephitis* and *Spilogale* and 6 bands in *Martes*. Each band extends from the lateral margin of the internal face of the sternum to the cartilage of the succeeding rib.

**Diaphragma.**—In each specimen this consists of the usual two sternocostal parts and the right and left parts of the dorsocentral crus.

**Obliquus abdominis externus.**—**ORIGIN:** *Mephitis* and *Spilogale*, by ten separate slips from last 10 ribs. *Martes*, similar slips from last 11 ribs and for a distance of 15 mm. posterior to last rib from lumbodorsal fascia. **INSERTION:** By thin aponeurosis into midventral line from xiphoid process to pelvic symphysis and on medial portion of anterior border of pubis. **REMARKS:** The muscle covers more of the obliquus abdominis internus in *Mephitis* than in *Spilogale* or *Martes*. It covers less of the last mentioned muscle in *Martes* than in either of the other two specimens. The amount of the obliquus abdominis internus covered is naturally determined by the position of the upper margin of the obliquus abdominis externus.

**Obliquus abdominis internus.**—**ORIGIN:** Lumbodorsal fascia, crural ligament extending to pectineal eminence, anterior border of ilium, and also in *Martes*, from anterior 15 mm. of ventral border of ilium. **INSERTION:** Midventral line by thin aponeurosis which, posteriorly, is single and passes ventral to rectus abdominis and, anteriorly, divides in usual manner and incloses the rectus abdominis.

**Transversus abdominis.**—**ORIGIN:** By fleshy fibers and sometimes aponeurosis from, all false and true ribs, diaphragma where fibers of two muscles interdigitate, tips of transverse processes of all lumbar vertebrae, anterior part of ventral margin of ilium, and crural ligaments. **INSERTION:** By aponeurosis to linea alba. **REMARKS:** Below the fourth lumbar vertebrae, at about the middle of the abdomen, the aponeurosis of one side measures in width, 18 mm. in *Mephitis*, 9 mm. in *Spilogale*, and 5 mm. in *Martes*.

**Rectus abdominis.**—**ORIGIN:** By strong tendon from anterior end of pelvic symphysis. **INSERTION:** By flat tendon on lateral face of first costal cartilage. *Mephitis* ventral four-fifths, *Spilogale* and *Martes* whole, of lateral face of first costal cartilage.

## MUSCLES OF THE SHOULDER AND UPPER ARM

**Spinodeltoideus.**—ORIGIN: posteroventral margin of metaeromion and spine of scapula, also fascia covering infraspinatus. INSERTION: By flat tendon on deltoid ridge of humerus.

**Acromiodeltoideus.**—ORIGIN: Lateral and ventral surfaces of acromion. INSERTION: By flat tendon, common to this muscle and spinodeltoideus, on deltoid ridge of humerus.

**Clavodeltoideus.**—ORIGIN: Clavicle and tendinous line of intersection between the clavodeltoideus and clavotrapezius muscles. INSERTION: A narrow line on anterior face of humerus.

**Supraspinatus.**—ORIGIN: Whole surface of supraspinatus fossa. INSERTION: Greater tuberosity of humerus.

**Infraspinatus.**—ORIGIN: Entire surface of infraspinatus fossa. INSERTION: Infraspinatus fossa of humerus, on greater tuberosity just lateral and ventral to insertion of supraspinatus.

**Teres minor.**—In *Mephitis* not differentiated from the infraspinatus. In *Spilogale* there is only a faint line separating the teres minor from the infraspinatus. In *Martes* the muscle is well defined and takes origin from the glenoid border of the scapula and infraspinatus muscle. It inserts on the greater tuberosity of the humerus immediately below the insertion of the infraspinatus.

**Subscapularis.**—ORIGIN: Subscapular fossa. INSERTION: Lesser tuberosity of humerus.

**Teres major.**—ORIGIN: Approximately posterior one-third of glenoid border of scapula. INSERTION: By flat tendon, common to this muscle and latissimus dorsi, on medial side of humerus beneath biceps brachii.

**Coracobrachialis.**—This muscle is present only in *Martes*. ORIGIN: By round tendon from anteromedial angle of coracoid process. INSERTION: By two heads: the first or short head, by fleshy fibers directly into medial side of humerus immediately below anterior border of lesser tuberosity; the second or long head, which takes origin by a long tendon from the tendon of the first head, by thin flat tendon on medial side of humerus along a line 11 mm. long which begins at a point 20 mm. below head of humerus. The second or long head is the larger of the two.

**Epitrochlearis.**—In *Mephitis* and *Spilogale* the anterior fibers of the caput longum of the triceps attach to the posterior one of the two heads of the latissimus dorsi. These fibers are few in *Mephitis*, and no

separation between them and the remainder of the caput longum of the triceps can be made out. In *Spilogale* more fibers attach to the caput longum than in *Mephitis*; but even here there is only a slight separation for a distance of 3 mm. at the origins of the museles. In *Martes* the muscle is represented by two parts, separate and distinct from one another and from any other muscle. Part *A* takes origin by a thin tendinous fascia from that head of the latissimus dorsi which inserts in front of the biceps brachii. Part *B* takes origin directly by muscle fibers from that head of the latissimus dorsi which inserts posteriorly to the biceps brachii. Both parts, which are much flattened, insert into fasciae that extend to the forearm. Part *B* is narrower but longer than part *A*. Part *B*, at its insertion, extends beneath part *A*; but the two parts are, even here, entirely distinct from one another.

**Biceps brachii.**—ORIGIN: By round tendon from tip of coracoid process. INSERTION: Bicipital tuberosity of radius.

**Brachialis.**—ORIGIN: Lateral surface of humerus from point just distal of teres minor tubercle to proximal end of supracondyloid ridge. INSERTION: By tendon on medial side of ulna immediately distal of semilunar notch.

**Caput laterale of triceps brachii.**—ORIGIN: Tubercle distal of infraspinatus fossa of humerus and into fossa immediately beneath head of humerus. INSERTION: Lateral face of olecranon. REMARKS: In *Mephitis* and *Spilogale* this is a separate and distinct muscle, but in *Martes* it is fused with the long portion of the caput mediale of the triceps brachii.

**Caput longum of biceps brachii.**—ORIGIN: Triangular area on axillary border of scapula immediately back of glenoid cavity. INSERTION: By strong tendon on rounded tuberosity of dorsal angle of olecranon. REMARKS: In *Mephitis* the area of origin extends up to within 1 mm. of the glenoid cavity. In the other two specimens it extends entirely to the glenoid cavity. The end of the ulna over which the tendon of this muscle passes to its insertion is most bifurcated in *Martes* and least bifurcated in *Mephitis*. Although the muscle is the same length in *Mephitis* as in *Martes*, in *Mephitis* it is much the heavier and less tendinous at both its origin and insertion.

**Caput mediale of triceps brachii.**—In two parts: Part *A*. Long head. ORIGIN: *Mephitis*, fossa immediately posterior to lesser tubercle under head, and postero-internal face of humerus for distance of 11 mm. below lower posterior margin of head. *Spilogale*, not reaching head of humerus but only postero-internal face of shaft of humerus for distance of 7.5 mm. beginning 2 mm. below posterior rim of head of humerus. *Martes*, part of head fused with caput laterale of triceps



brachii. Origin otherwise essentially as in *Mephitis* except that area of insertion extends below posterior margin of head of humerus on shaft of humerus for a distance of 15 mm. INSERTION: Postero-internal face of olecranon. Part *B*. Short head. ORIGIN: In *Mephitis* and *Spilogale* posteromedial (toward body) one-fourth, and in *Martes*, one-half, of posterior face of medial epicondyle of humerus. INSERTION: Medial side of olecranon immediately behind posterior margin of semilunar notch.

**Caput anguli of triceps brachii.**—ORIGIN: Posterior end of glenoid border of scapula. INSERTION: By flat tendon which passes over tip of olecranon and inserts on posterior rounded surface of olecranon. REMARKS: Near its origin a tough fascia binds this muscle closely to the teres major. The muscle is apparently uniformly present in, and peculiar to, the Mustelidae. The term, caput anguli, here proposed for the muscle, has reference to its origin which is from the postero-ventral angle of the scapula.

**Anconeus.**—ORIGIN: Dorsal half of lateral epicondyle and triangular area on posterior side of distal end of humerus. INSERTION: Dorsolateral face of olecranon from tip of same to distal margin of semilunar notch. REMARKS: The muscle is actually about the same size in *Spilogale* as in *Martes*. In *Mephitis* it is about three times as large as in either of the other two specimens. In *Mephitis* and *Spilogale* the area of origin extends over slightly more than, and in *Martes* slightly less than, half the length of the humerus.

## MUSCLES OF THE FOREARM

**Brachioradialis.**—ORIGIN: Anterior face of dorsal margin of supracondyloid ridge. INSERTION: By thin, flat, fascia-like tendon to styloid process of radius and ligaments adjacent to styloid process.

**Extensor carpi radialis longus.**—ORIGIN: Anterior face of supracondyloid ridge immediately below origin of brachioradialis. INSERTION: By two tendons which insert on bases (proximal ends) of second and third metacarpals. REMARKS: The tendon inserting on the third metacarpal is, in *Mephitis* 3 times, but in *Martes* only  $1\frac{1}{4}$  times, as wide as the tendon inserting on the second metacarpal.

**Extensor digitorum communis.**—ORIGIN: Supracondyloid ridge immediately below origin of extensor carpi radialis longus. INSERTION: By tendons on proximal ends of first phalanges of second to fifth digits. The tendons also continue on to the proximal ends of the last phalanges of the second to fifth digits.

**Extensor digitorum lateralis.**—ORIGIN: Ventral portion of anterior face of supracondyloid ridge of humerus. INSERTION: On digits 3, 4 and 5 by three tendons which join ulnar sides of tendons of extensor digitorum communis on these digits and insert with them.

**Extensor carpi ulnaris.**—ORIGIN: Lateral epicondyle of humerus. In *Martes* also from ridge at dorsal tip of semilunar notch of ulna. INSERTION: By broad flat tendon on lateral side of base of fifth metacarpal.

**Extensor indicis.**—ORIGIN: *Mephitis*, lateral surface of ulna from posterior extent of semilunar notch to point three-fifths of way distally on ulna. *Martes*, the same except that area of origin extends proximally only as far as anterior border of semilunar notch, and the muscle is fused with the extensor brevis pollicis. INSERTION: By two tendons which continue to ends of first and second digits but also insert strongly on head of first phalanx of first and second digits.

**Supinator.**—ORIGIN: Lateral side of angular ligament of radius. INSERTION: dorsal and medial faces of radius forward as far as posterior end of line of insertion of pronator teres.

**Extensor pollicis brevis.**—ORIGIN: *Mephitis*, lateral face of proximal seven-tenths of radius and anterior face of ulna from lower end of semilunar notch to within 8 mm. of distal end of ulna. *Martes*, the same except for extension to within 5 mm. of distal end of ulna. INSERTION: By strong tendon on lateral face of base of first metacarpal.

**Pronator teres.**—ORIGIN: Extremity of internal epicondyle of humerus. INSERTION: Medial side of radius. *Mephitis*, by flat tendon 12 mm. wide. *Spilogale* and *Martes*, by flat tendon and fleshy fibers. REMARKS: In *Martes* this muscle is intimately fused with the flexor carpi radialis for a short distance beginning at a point 4 mm. distal of the origin of both. In fact some fibers of the former insert as part of the pronator teres. The length of the line of insertion is: in *Martes* 10 mm., in *Spilogale* 5 mm., in *Mephitis* 12 mm. In all three specimens the line of insertion begins distally to the middle of the radius.

**Flexor carpi radialis.**—ORIGIN: Tip of median epicondyle of humerus. INSERTION: Into bases of second and third metacarpals by slender tendon that passes through groove between os magnum and first metacarpal.

**Palmaris longus.**—ORIGIN: Distal part of medial surface of medial epicondyle of humerus. A second part, *B*, takes origin from the lateral side of the humeral head of the muscle at about the middle of the forearm. In *Mephitis* the origin of part *B* is by a flat tendon and the two parts of the muscle are distinct throughout, but in *Martes*

the two are fused almost to the wrist. INSERTION: Part *B*. This continues as a fleshy bundle as far as the middle of the metacarpals, at which place it becomes tendinous and inserts by a strong tendon into the base of the first phalanx of the fifth digit. A tendon is also given off to the fibrous pad which overlies the sesamoid bone. In *Martes* a few fibers also arise from the transverse ligament of the wrist and insert with this muscle. This is similar to the arrangement described in the cat by Reighard and Jennings (1901, p. 181) where this muscle is described as the ulnar part of the flexor sublimus digitorum. In *Mephitis* all the fibers come from the palmaris longus, none from the transverse ligament of the wrist. Part *A*. This part becomes a single strong tendon, in *Mephitis* at the middle of the forearm, in *Martes* 5 mm. from the wrist. This tendon passes deep to the tendon given off by part *B* to the fibrous pad overlying the sesamoid bone and is enclosed in the transverse ligament of the wrist. In *Mephitis* this tendon spreads out in the palm of the hand into a broad, single sheet that breaks up into three parts which insert on the bases of the first phalanges of the second to fourth digits. The tendon on the fourth digit of *Mephitis* that inserts on the base of the first phalanx also continues laterally and inserts on the base of the third or distal phalanx of the fifth digit. In *Martes* no broad sheet is formed in the palm of the hand. Instead, the tendon divides immediately after passing the transverse ligament of the wrist.

. **Flexor carpi ulnaris.**—ORIGIN: Lateral surface of olecranon. INSERTION: Proximal portion of pisiform bone. *Mephitis*, by tendon 12 mm. long. *Martes*, by tendon less than 1 mm. long but twice as wide as that in *Mephitis*. REMARKS: Near the origin there is some fusion with the flexor profundus in *Mephitis*; but in *Martes* the muscle is distinct and separate from any other muscle.

**Flexor digitorum sublimis.**—ORIGIN: Second and third heads of flexor digitorum profundus and common tendon formed by these two heads. INSERTION: The muscle divides into two tendons in passing through the hollow of the common tendon of the flexor digitorum profundus. The lateral one of the two tendons divides again. The three tendons thus formed extend to the pulley rings at the bases of the first phalanges of the second, third, and fourth digits, where they insert. On each of these three digits two tendons, one on either side of the tendon of the flexor digitorum profundus, extend from the pulley ring at the base of the second phalanx. If these be regarded as continuations of the flexor sublimus digitorum they may properly be said to be pierced by the tendon of the flexor digitorum profundus. The facts are that each of the two tendons that extend from the base of the first to the base of the second phalanx is larger than the single tendon of the flexor sublimus digitorum that extends from the wrist

to the pulley ring at the base of the first phalanx. Thus but a small part, if any part, of the two tendons, extending between the bases of the first and second phalanges, can be said to be a direct continuation of the tendon of the flexor sublimus digitorum.

**Flexor digitorum profundus.**—**ORIGIN:** By five heads which unite in the wrist to form one large flexor tendon. Part *A*. Posteromedial face of ulna from proximal lip of sigmoid cavity to within 5 mm. of styloid process. **REMARKS:** In *Mephitis* the distal half and in *Martes* the distal fourth of this head is fused on its radial face with the fifth head. The tendon of the first head forms the ulnar side of the common tendon in the wrist. Part *B*. Distal end of medial epicondyle of humerus. **REMARKS:** The tendon forms the median and dorsal (viewed from palmar surface) part of the common tendon in the wrist. In *Mephitis*, from its origin to a point 15 mm. distal to the origin, this head is fused with the third head. In *Martes* the second head is entirely distinct at and near its origin but fuses with the tendon of the third head at a point farther proximally on the forearm than in *Mephitis*. Part *C*. Distomedial or peripheral angle of median epicondyle of humerus. **REMARKS:** Its tendon forms the radial side of the common tendon in the wrist. Part *D*. By strong tendon, short and flat in *Mephitis*, long and slender in *Martes*, from median epicondyle of humerus just proximal of area of origin of second head. **REMARKS:** The tendon of the fourth head passes ventrally (viewed from palmar surface) to the tendon of the second head and forms part of the medial portion of the common tendon in the wrist. Part *E*. Medial third of ventral surface of ulna and slightly more than medial third of radius. **REMARKS:** The muscle extends proximally on the radius to the tendon of the biceps brachii. The muscle is fleshy and can perhaps more properly be said to insert on the common tendon formed by the union of the tendons of the other heads, than to contribute a separate tendon to the common tendon. **INSERTION:** The palmar surface of the common tendon in the wrist is nearly flat in *Martes*, but in *Mephitis* it is concave and forms a half-ring. It divides into five tendons which insert into the bases of the terminal phalanges of the five digits. In both specimens a tough ligamentous pulley ring surrounds the common tendon of the flexor profundus digitorum in the wrist. In *Martes* three tendons extend out from the palmar side of this flat ligamentous pulley ring at the base of the first phalanx of the second to fourth digits. Thus they lie on the ventral or palmar side of the tendons of the flexor digitorum sublimus which extend to the same points of insertion.

**Pronator quadratus.**—**ORIGIN:** By fleshy fibers from distal fourth of flexor surface of ulna. **INSERTION:** By fleshy fibers into distal surface of flexor surface of radius.

## MUSCLES OF THE HAND

**Lumbricales.**—ORIGIN: By fleshy fibers from palmar surface of common tendon of flexor digitorum profundus. INSERTION: By thin tendons. In *Mephitis*, by three heads: one on radial side of third digit and other two on radial and ulnar sides of fourth digit. In *Martes* by four heads, one each on radial side of upper third of first phalanx of second to fifth digits. REMARKS: The muscles in *Mephitis* also insert into the upper third of the first phalanges. As well as being one more in number in *Martes*, the individual muscles are larger than in *Mephitis*. Also, in *Mephitis*, the muscles have a common origin whereas each slip arises separately in *Martes*.

**Adductor pollicis brevis.**—ORIGIN: Distal border of calcareous, transverse ligament which extends from fibrous pad lying over pisiform bone to radial border of hand. INSERTION: By slender tendon into base of first phalanx of first digit on palmar surface. REMARKS: This muscle is larger in *Martes* than in *Mephitis*. In the latter it takes origin mostly from the fibrous pad overlying the pisiform bone and center of the wrist and extends mesially only about half way between the fibrous pad and the radial border of the hand.

**Flexor pollicis brevis.**—ORIGIN: Borders of os magnum and scapholunar adjacent to one another and fascia between the two. INSERTION: By short tendon into base of first phalanx.

**Adductor pollicis.**—ORIGIN: By fleshy fibers from os magnum and fascia extending over palmar surface of carpal bones. INSERTION: Ulnar side of first phalanx of pollex. REMARKS: This is a heavier muscle than the flexor pollicis brevis.

**Interossei.**—ORIGINS: By fleshy fibers from palmar surfaces of bases of second to fifth metacarpals. INSERTIONS: Each of the four on both ulnar and radial sides of first phalanx of digit from which it takes origin.

**Adductor digiti secundi.**—Two muscles may be included under this name. (a) ORIGIN: Trapezium. INSERTION: Radial side of base of first phalanx of second digit. (b) ORIGIN: Os magnum and fascia overlying it. INSERTION: Ulnar side of base of first phalanx of second digit. REMARKS: These two muscles together with the adductor digiti quinti and opponens (adductor) digiti quinti constitute a layer overlying (in palmar view) the interossei muscles.

**Adductor digiti quinti.**—ORIGIN: Distal surface of pisiform bone. INSERTION: By tendon into ulnar side of base of first phalanx of fifth digit.

**Flexor digiti quinti brevis.**—ORIGIN: From ligament which surrounds common tendon of flexor digitorum profundus. INSERTION: By flat tendon into base of first phalanx of fifth digit. REMARKS: This is entirely distinct from the underlying (in palmar view) interossei muscles of this digit.

**Opponeus digiti quinti.**—ORIGIN: Os magnum and fascia covering it. INSERTION: Ulnar side of base of first phalanx of fifth digit.

## MUSCLES OF THE ANUS AND SCENT GLANDS

**Director ani superior.**—ORIGIN: Transverse tendinous intersection in semitendinosus 16 mm. below origin of same and adjacent margins of gracilis and biceps femoris. INSERTION: Lateral margin of anus. REMARKS: The muscle is not present in *Martes*. In *Spilogale* 5 mm. of it remains at the origin and indicates that it was relatively as well developed as in *Mephitis*. In *Mephitis* the muscle is 36 mm. long, 11 mm. wide at its origin which is 2 mm. wider than the semitendinosus, 18 mm. wide at its insertion, and nearly 2 mm. thick. The semitendinosus is more firmly joined by fascia to the deeper lying semimembranosus than in *Martes*. The muscle is not regarded as the homologue of any of the numerous small anal muscles because it lies lateral to the levator ani which, excepting the transversus perinei, is the outermost of the anal muscles. The levator ani is present in both *Mephitis* and *Martes*. The transversus perinei, however, was not found in its usual position in either specimen. This leads one to suspect that it has become modified. If so, it would appear more probable that it has fused with the sphincter ani internus to form the muscle sheath of the anal scent gland, or perhaps that it represents the muscle here called the director ani inferior, than that it has given rise to the director ani superior. The possibility that the director ani superior represents the caudal head of the semitendinosus has suggested itself. Among the Mustelidae, the caudal head of the semitendinosus is only known to be absent in *Mephitis*, *Spilogale*, *Meles taxus* and *Ictonyx zorilla*. Unfortunately the innervation of this and the surrounding muscles was destroyed in removing the skin and fat, and evidence from this important source cannot be presented. The name, director ani superior, here coined, refers to the muscle's function. It evidently directs or points the anal papillae of the scent glands in the desired direction. The director ani inferior assists it in doing this.

**Director ani inferior.**—ORIGIN: Ramus of ischium immediately above symphysis and anterior to ischiocavernosus. INSERTION. Posterodorsal surface of sphincter ani internus which covers the anal

scent glands. **REMARKS:** The muscle is 4 mm. wide in *Martes*. It is entirely separate from the levator ani, arising posteriorly to it. In thickness, manner of origin, and general direction of fibers it is much like the levator ani. In *Mephitis* it is a large flat muscle, 42 mm. long and about 4 mm. in diameter, except at its insertion where it becomes flattened and is 16 mm. wide. Its function is apparently also that of pointing the anal papillae in the desired direction, but the pull is exerted in a different direction than is the pull of the director ani superior. It may possibly be homologous with the transversus perinei. (See remarks under preceding muscle.)

**Sphincter ani internus.**—In *Mephitis* the large, thick muscle whose fibers extend dorsoventrally over the posterior three-fourths of the anal scent gland is regarded as the sphincter ani internus. Dorsally the muscles of the two sides are continuous over the top and posterior sides of the glands. Ventrally the muscles attach to the heavy, vertical sheet of fascia that extends from the symphysis of the ischium to the anal apparatus. The muscles are present in *Martes* but relative to those in *Mephitis* are small, and dorsally they attach to the fascia connecting the anal apparatus with the tail. This muscle is evidently what Chatin (1874, p. 18) speaks of as the second or deep layer in the tunic which surrounds the anal scent glands of skunks. Chatin's information was evidently gained from the dissection of a species of *Conepatus* which might differ from *Mephitis*. In the specimen of *Mephitis* dissected by the author the so-called outer layer comprises only the expanded ends of the director ani superior and inferior which, actually, cover less than half of the gland.

**Caudoanalis and caudocavernosus.**—In *Martes* the two are inseparable. They extend from the ventral surface of the first caudal vertebra to the corpus cavernosum. In *Mephitis* the large, thick muscle overlying the posterior surface of the anal scent gland apparently corresponds to one or both of these muscles.

**Sphincter ani externus.**—A thin, narrow band of muscle fibers extending around the margin of the anal orifice and lying beneath the insertion of the director ani superior is regarded as representing this muscle. In *Martes* it is apparently fused with the sphincter ani internus. This and the four preceding muscles constitute all those actually connected with the anal scent glands of *Mephitis*.

**Caudorectalis.**—**ORIGIN:** Ventral face of third caudal vertebra. **INSERTION:** Dorsal and lateral face of rectum. **REMARKS:** The origin is heavier in *Martes* than in *Mephitis*; but after passing onto the intestine where its fibers extend longitudinally it is thicker in *Mephitis* than in *Martes*. Beneath the caudorectalis there is a second muscle, also much heavier in *Mephitis* than in *Martes*, whose fibers are at right angles with those of the caudorectalis and which encircle the rectum.

**Compressor urethrae membranaceae.**—In *Mephitis* the fibers encircle the urethra between Cowper's glands and the prostate. In *Martes* this same part of the urethra is covered with muscle fibers which, however, extend longitudinally.

**Levator ani.**—ORIGIN: *Mephitis*, from fascia, covering Cowper's glands and extending down to symphysis. *Martes*, by fleshy fibers from symphysis of ischium. INSERTION: *Mephitis*, fascia covering dorsal surface of rectum and ventral surface of tail. *Martes*, ventral face of second and third caudal vertebrae. REMARKS: The muscle is 13 mm. wide in *Mephitis* and 8 mm. wide in *Martes*. It is, however, much thicker in *Martes* than in *Mephitis*.

**Ischiocavernosus.**—ORIGIN: Caudal border of ramus of ischium. INSERTION: Bulb of corpus cavernosum penis. REMARKS: The muscle is well developed in both specimens, but begins its insertion nearer the ischial tuberosity in *Martes* than in *Mephitis*.

### MUSCLES OF THE HIP AND THIGH

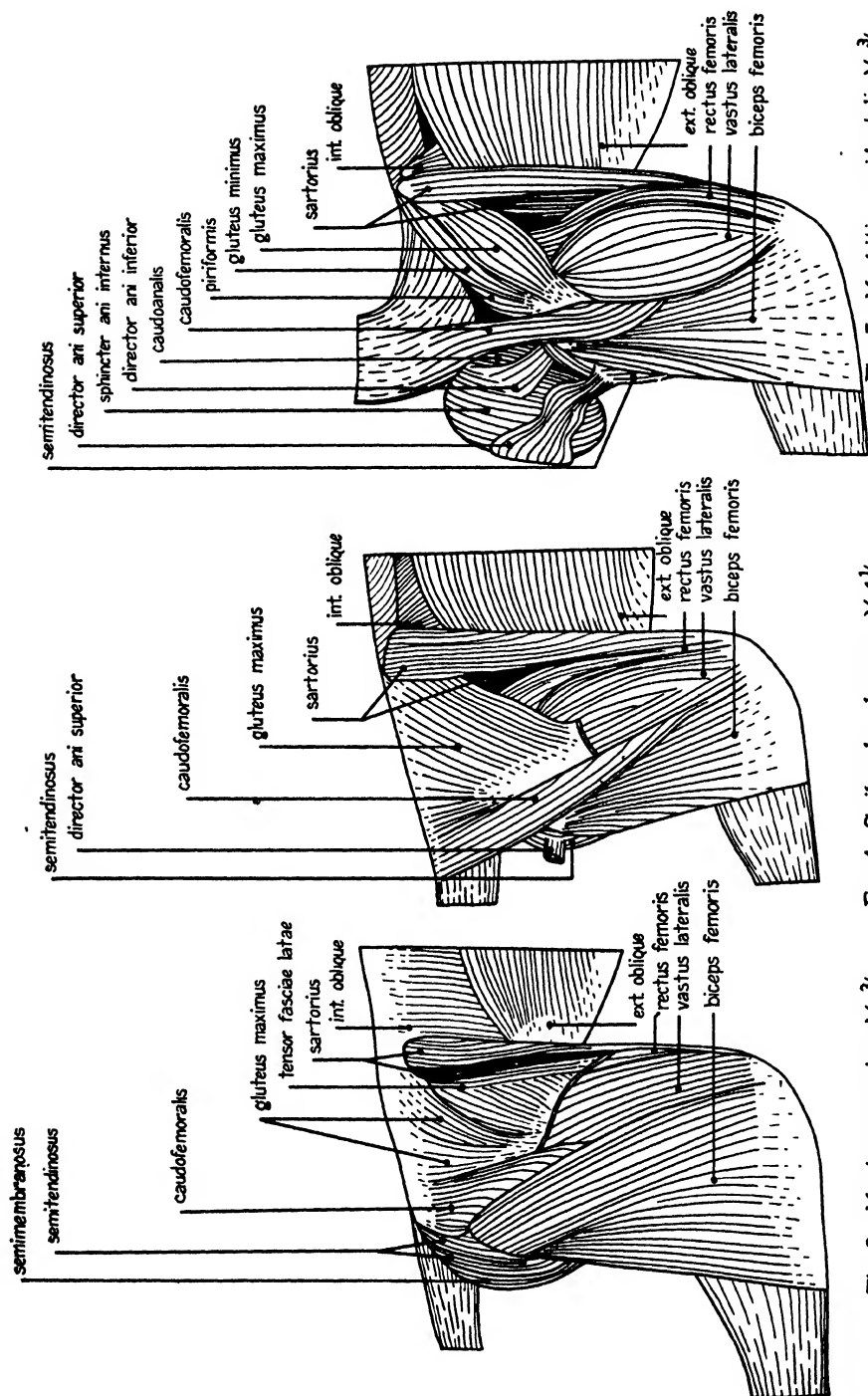
**Tensor fasciae latae.**—Present only in *Martes*. ORIGIN: Anterior fibers from ventral border of ilium. Remainder from fascia covering ventral border of gluteus maximus. INSERTION: Into fasciae latae. REMARKS: No trace of this muscle is present in *Mephitis*. The muscle is also absent in *Spilogale*, but the gluteus maximus inserts partly into the fasciae latae as well as on the femur.

**Gluteus maximus.**—ORIGIN: *Mephitis*, by flat tendon 6 mm. wide from anteroposterior margin of ilium. *Spilogale* and *Martes*, from fascia covering gluteus medius, from fascia covering spinalis muscles, and by thin tendon from transverse processes of last sacral and first two caudal vertebrae. INSERTION: Caudal side of ridge that extends distally from greater trochanter. REMARKS: In *Martes* this muscle is slightly fused with the caudofemoralis.

**Gluteus medius.**—ORIGIN: Anterodorsal face of ilium. In *Spilogale* and *Martes* also from fascia covering spinalis muscles. The latter region of origin is more extensive in *Martes* than in *Spilogale*. INSERTION: Proximal end of greater trochanter.

**Piriformis.**—ORIGIN: *Mephitis* and *Spilogale*, transverse processes of last sacral and first two caudal vertebrae (regarding the sacrum of *Mephitis* and *Spilogale* as composed of two vertebrae). *Martes*, transverse processes of last two sacral and first caudal vertebrae. This muscle is five times as large in *Mephitis* as in *Martes*. It is twice as large in *Martes* as in *Spilogale*.



Fig. 5. *Mephitis occidentalis* X  $\frac{2}{5}$ Fig. 4. *Spilogale phenax*, X  $1\frac{1}{3}$ Fig. 3. *Martes caurina*, X  $\frac{3}{4}$

**Gemelli.**—ORIGIN: Dorsal border of ischium from tuberosity, anteriorly, to posterior border of iliocapsularis. INSERTION: In common with obturator internus into proximal end of trochanteric fossa. REMARKS: The two gemelli are continuous with one another and lie ventrally to the distal part of the obturator internus but project from beneath its tendon both anteriorly and posteriorly.

**Iliocapsularis.**—This lies between the gluteus minimus and the gemellus superior. ORIGIN: Dorso-internal margin of pelvis from ilium and ischium mesial to anterior half of acetabulum. INSERTION: Anterior and dorsal part of lateral face of greater trochanter.

**Gluteus minimus.**—ORIGIN: Lateral face of ilium, slightly ventral and mostly posterior to area of origin of gluteus medius. *Mephitis*, posterior extension of area of origin lacks 2 mm. of reaching anterior apex of triangular area of insertion of rectus femoris. *Spilogale* and *Martes*, area of origin extends posteriorly to apex of above mentioned triangular area. INSERTION: Anteroventral part of lateral face of greater trochanter of femur. REMARKS: At its origin this muscle is separate from the iliocapsularis in *Mephitis* and *Martes* but not in *Spilogale* where the two muscles are continuous throughout.

**Quadratus femoris.**—ORIGIN: Triangular area on lateral surface of ischium below ischial tuberosity. INSERTION: *Mephitis*, medial half of posterior surface of shaft of femur. *Spilogale*, transversely elliptical area extending from lesser trochanter to lateral margin of femur at lower margin of greater trochanter, thus being ventral to the trochanteric fossa. *Martes*, by stout, thick tendon into distal end of trochanteric fossa. REMARKS: In so far as known to the writer the area of insertion in *Mephitis* is larger, relative to the size of the femur, than in any other member of the Carnivora.

**Obturator externus.**—ORIGIN: Lateral face of posterior ramus of ischium and ventral ramus of ischium and pubis adjacent to obturator foramen. INSERTION: By short, stout tendon into trochanteric fossa proximal to area of insertion of quadratus femoris.

**Obturator internus.**—ORIGIN: Medial face of innominate on posterior and ventral margins of obturator foramen. INSERTION: In common with gemelli into proximal end of trochanteric fossa.

**Biceps femoris.**—ORIGIN: By short tendon from lateral face of ischial tuberosity. INSERTION: By broad tendon on patella and lateral surface of lower leg. *Mephitis*, proximal half of leg. *Spilogale* and *Martes*, slightly more than proximal third of leg.

**Tenuissimus.**—ORIGIN: *Martes*, transverse process of first caudal vertebra. *Spilogale*, insertion damaged but apparently as in *Martes*. Perhaps from second caudal. INSERTION: Fascia on lower surface of lower leg at posterior border of biceps femoris. REMARKS: The muscle

is absent in both limbs of *Mephitis*. It was 1 mm. wide in *Spilogale* and 2.8 mm. wide in *Martes*.

**Caudofemoralis.**—ORIGIN: *Mephitis* and *Spilogale*, by flat tendon from transverse process of fourth caudal vertebra and by fascia from side of tail. *Martes*, from transverse process of first caudal and possibly last sacral vertebra. INSERTION: Lateral face of femur on line with line of insertion of fibers of gluteus maximus that extend farthest distally. *Mephitis*, wholly by thin, flat tendon, the muscle fibers terminating 10 mm. short of actual line of insertion. Line of insertion is 18 mm. long and begins 20 mm. proximal to distal end of femur. Femur 63 mm. long. *Spilogale* and *Martes*, by fleshy fibers. *Spilogale*, line of insertion extends onto lateral condyle of femur. *Martes*, continuous proximally with that of gluteus maximus and distally with that of presemimembranosus. More exactly the fibers insert from a point 14 mm. below the head of the femur to a point 18 mm. above the distal end of the femur, the femur itself being 70 mm. long.

**Semitendinosus.**—ORIGIN: Ischial tuberosity, and in *Martes* by a second head from fascia covering spinous muscles at second caudal vertebra. INSERTION: Medial side of cnemial crest just distal to insertion of gracilis. Certainly, in *Martes*, the insertion extends on over the tendon of Achilles. REMARKS: Although no caudal head is present in *Mephitis* and *Spilogale*, the director and superior extending to the anal scent gland may represent the caudal head which has migrated onto the lateral face of the scent gland.

**Semimembranosus.**—ORIGIN: Caudal border of tuberosity and ramus of ischium. INSERTION: Femur immediately above internal condyle and internal condyle of tibia. REMARKS: The two parts corresponding to the two areas of insertion are separated farthest proximally in *Spilogale*.

**Presemimembranosus.**—Present only in *Martes*. ORIGIN: Transverse process of second caudal vertebra. Adjacent to, but distinct from, caudal head of semitendinosus at origin. INSERTION: Distal part of lateral surface of medial third of femur immediately posterior to line of insertion of caudofemoralis. REMARKS: The muscle is 2.8 mm. wide, exactly the same width as the tenuissimus. Although the presemimembranosus is present in many of the Carnivora, the one in this specimen of *Martes* is unique in having a caudal origin and an insertion more proximal than, at least, is usually the case. It is entirely distinct and has the usual sciatic innervation.

**Sartorius.**—ORIGIN: Ventral half of crest of ilium and ventral margin of ilium. *Mephitis* and *Spilogale*, posteriorly to anterior border of gluteus maximus. *Martes*, posteriorly to anterior border of tensor fasciae latae. *Martes*, posterior third of origin by thin tendon.

**INSERTION:** By thin tendon whose insertion begins at proximal end of patella, extends distally over patella, thence across ligaments on medial side of knee and into tibia on medial side of anterior crest. **REMARKS:** The muscle is single.

**Gracilis.**—**ORIGIN:** *Mephitis* and *Spilogale*, ischial symphysis and inferior border of pubis as far anteriorly as pectineal eminence. *Martes*, broad flat tendon from symphysis. **INSERTION:** By thin flat tendon on medial side of anterior crest of tibia immediately distal to insertion of sartorius. **REMARKS:** In *Martes* the muscle is tendinous some distance from both its insertion and origin and in this respect is most different from the corresponding muscle in *Mephitis* and *Spilogale*.

**Adductor mass.**—**ORIGIN:** Ischial symphysis and anteriorly to posterior margin of pectineus. **INSERTION:** Postero-internal margin of femur. **REMARKS:** Distally, in *Martes* and *Spilogale*, the area of insertion is V-shaped, but in *Mephitis* it is only slightly so since the muscle does not extend distally to the condyles.

**Pectineus.**—**ORIGIN:** Pectineal eminence. **INSERTION:** By thin, flat tendon into posteromedial face of shaft of femur immediately anterior to insertion of main adductor mass. **REMARKS:** In *Spilogale* and *Martes* the posterior part of the muscle is faintly divided from the remainder. The insertion of the posterior part is continuous with, actually a part of, the line of insertion of the pectineus and not part of the adductor mass. Also in *Martes* this portion arises from the pectineal eminence. In *Spilogale* the posterior part arises from behind the pectineal eminence. The pectineus would appear to be bilaminar, at least in *Martes*.

**Rectus femoris.**—**ORIGIN:** By strong tendon from triangular area whose base is at anterior margin of acetabulum. **INSERTION:** Median outer face of patella near its proximal border.

**Vastus lateralis.**—**ORIGIN:** Dorsal and lateral faces of shaft of femur. *Martes*, a restricted area at proximal end of femur. **INSERTION:** Lateral margin of patella. **REMARKS:** The area of origin is actually in *Mephitis* and relatively in *Spilogale* four times as extensive as in *Martes*. The muscle is fused with the vastus medialis in *Mephitis* and *Spilogale*, but is distinct and separate in *Martes*.

**Vastus medialis.**—**ORIGIN:** Triangular area below head of femur. **INSERTION:** Medial face and margin of patella.

**Vastus intermedius.**—**ORIGIN:** Anterior face of femur between areas of insertion of vastus medialis and vastus lateralis. **INSERTION:** Medial part of proximal border of patella. **REMARKS:** The muscle is distinct throughout. The quadriceps femoris is divided into four distinct parts in *Martes*, and the areas of insertion are smaller than in *Mephitis* or *Spilogale*. The fusion of the parts is greatest in *Mephitis*.

## MUSCLES OF LOWER LEG AND FOOT

**Gastrocnemius.**—ORIGIN: By two heads. One head from above each condyle on posterior face of femur. INSERTION: Proximal end of calcaneus. REMARKS: In *Mephitis* the two heads are joined by fascia throughout their distal half and in *Martes* throughout their distal two-thirds. In *Mephitis* in its distal third the medial head overlaps the lateral head. Proximally, in *Martes*, the plantaris is fused with the lateral head. In *Mephitis* there is no fusion of plantaris with gastrocnemius except that their tendons are united with one another distally. No fabellae were present in either specimen.

**Plantaris.**—ORIGIN: In common with lateral head of gastrocnemius from posterior surface of femur immediately above lateral condyle. INSERTION: The tendon passes on over the calcaneus, being inclosed in the sheath formed by the tendons of the gastrocnemius and soleus, and widens out into the flexor brevis digitorum.

**Soleus.**—ORIGIN: Posterolateral face of head of fibula. INSERTION: Proximal part of calcaneus. REMARKS: The muscle is three times as large in *Mephitis* as in *Martes*. The tendon by which it takes origin is 3 mm. long and 4 mm. wide in *Mephitis* and 11 mm. long and 1 mm. wide in *Martes*. The tendon by which it inserts is 10 mm. long in *Mephitis* but less than 1 mm. long in *Martes*. In each the muscle joins the gastrocnemius 10 mm. proximal to the insertion.

**Popliteus.**—ORIGIN: By strong tendon from lateral epicondyle of femur. INSERTION: Proximal posteromedial face of tibia; in *Mephitis* proximal one-fourth and in *Martes* proximal one-third. REMARKS: No sesamoid was present in the tendon.

**Flexor digitorum longus.**—ORIGIN: All but distal one-eighth of medial face of fibula and distal four-fifths of lateral face of tibia. INSERTION: After union with tendon of tibialis posterior, by five strong tendons which insert in same manner as those of flexor digitorum profundus of hand.

**Flexor hallucis longus.**—ORIGIN: Head of fibula; also, in *Mephitis*, all but proximal 12 mm. of proximal half of posterior face of tibia, and in *Martes*, distal half of proximal fourth of posterior face of tibia. INSERTION: *Mephitis*, navicular and head of first metatarsal. *Martes*, entocuneiform.

**Tibialis posterior.**—ORIGIN: *Mephitis*, head of fibula and posterior face of tibia from point 12 mm. distal to head to middle of tibia.

*Martes*, head of fibula and posterior face of tibia from point 10 mm. distal to head to slightly below middle of tibia. INSERTION: Joins tendon of flexor digitorum longus.

**Peroneus longus.**—ORIGIN: Anterolateral face of head of fibula. *Mephitis*, also a few fibers from head of tibia. INSERTION: Bases of fifth and first metatarsals.

**Peroneus quinti brevis (peroneus tertius).**—ORIGIN: Lateral face of shaft of fibula. *Mephitis*, proximal fourth. *Martes*, second fourth, proceeding distally. INSERTION: By slender tendon into base of second phalanx of fifth digit where fusion occurs with tendon of extensor digitorum longus.

**Peroneus brevis.**—ORIGIN: *Mephitis*, middle third of lateral surface of shaft of fibula. *Martes*, proximal two-thirds of distal half of lateral face of shaft of fibula. INSERTION: Base of fifth metatarsal.

**Extensor digitorum longus.**—ORIGIN: By tendon from lateral epicondyle of femur. INSERTION: By four tendons on dorsal surfaces of bases of second phalanges of second to fifth digits.

**Tibialis anterior.**—ORIGIN: Proximal 20 mm. of lateral face of tibia, head of fibula, and in *Mephitis* proximal 12 mm. and in *Martes* proximal 45 mm. of medial face of fibula. INSERTION: By tendon on medial side of first metatarsal.

**Extensor digitorum brevis.**—ORIGIN: *Mephitis*, lateral face of calcaneus. *Martes*, dorsal surface of calcaneus. INSERTION: By tendons into lateral sides of first to fourth digits. REMARKS: These tendons fuse with those of the extensor digitorum longus. In *Mephitis* the tendon to the first digit sends a branch to the side of the second digit. In *Martes* the tendon to the third digit gives off a slender branch to the medial side of the fourth digit. Thus the second digit of *Mephitis* and the fourth digit of *Martes* each have two tendons, one on each side. The extra tendons are relatively small and possibly are not constant.

**Flexor digitorum brevis.**—ORIGIN: Distal end of tendon of plantaris. INSERTION: Bases of second phalanges of second to fifth digits. REMARKS: The muscle is fleshy for only the two lateral tendons in *Martes*. In *Mephitis* it is fleshy for all. The four tendons form the flexores perforati for the four outer toes. Each forms a fibrous ring at the base of the first phalanx, whence the tendon is divided into two parts which insert, one on either side of the first phalanx.

**Accessorius.**—ORIGIN: Ventral and lateral face of calcaneus. INSERTION: Conjoined tendons of flexor digitorum longus and tibialis posterior. REMARKS: In *Martes* its bulk is three times that in *Mephitis*. In the latter both the tendon of origin and the tendon of insertion

are weak. In *Martes* the origin is by fleshy fibers over nearly the whole of the lateral face of the calcaneus as far posteriorly as the articulation with the tibia, and the tendon of insertion is strong and 5.5 mm. wide.

**Lumbricales.**—Four are present in *Martes* but only three in *Mephitis*. **ORIGIN:** Plantar side of tendon of flexor digitorum longus. **INSERTION:** *Mephitis*, medial side of three lateral digits at heads of metacarpals. *Martes*, each of the three lateral muscles has two insertions. One part of each ends in tendon that extends along ventral side of large tendon of flexor digitorum longus to head of metatarsal where it forms part of sheath for latter. The second parts of the three lateral muscles and all of the fourth or medial muscle insert on the medial sides of the four lateral digits at the heads of the metatarsals. The inner muscle is less than half as large as any one of the three lateral ones.

**Adductor ossis metatarsi quinti (calcaneometatarsalis).**—**ORIGIN:** Ventral surface of calcaneus near posterior end. **INSERTION:** Ventral surface of fifth metatarsal. **REMARKS:** The muscle is three times as large in *Mephitis* as in *Martes*.

**Adductor muscles of foot, first deep layer.**—There are three adductors, one each to the first, second, and fifth digits.

**Adductor muscles of foot, second deep layer.**—In addition to the following foot muscles there is a flexor brevis for each of the first four digits.

**Abductor and adductor medius digiti quinti.**—**ORIGIN:** Head of fifth metatarsal. **INSERTIONS:** Respectively, lateral and medial side of head of first phalanx of fifth digit.

**Adductor medius digiti pollicis.**—**ORIGIN:** By tendon from internal cuneiform and by second tendon from base of first metatarsal. **INSERTION:** Ventrolateral side of base of first phalanx of first digit. **REMARKS:** This might be considered as two muscles were it not for the fact that the two parts have the same insertion.

## SUMMARY

Although, as stated in the introduction, no attempt is made to classify the genera of the Mustelidae on a basis of their musculature, it seems useful to point out the following differences between the three whose musculature has just been described. As will readily be apparent from the preceding detailed account, the following mentioned differences are only a few of the total number. These selected few are probably constant and, at least most of them, are of use taxonomically.

*Mephitis* differs from both *Spilogale* and *Martes* in the following respects: The undifferentiated condition of: the psoas muscles, the adductor mass, the quadriceps femoris, the sternomastoideus, and the teres minor from the subscapularis. The absence of the tenuissimus. The smaller size of the accessorius and gluteus maximus. The larger size of the piriformis. The larger area of insertion of the quadratus femoris.

In addition, *Spilogale* differs from *Mephitis* in the following points: The absence of the omohyoid and part 1 of the scalenus longus. The relatively larger size of the serratus posterior superior. The more extensive origin of the spinotrapezius and clavotrapezius.

Points in which both *Mephitis* and *Spilogale* differ from *Martes* are as follows: Undifferentiated condition of the psoas muscles. Absence of longissimus capitis, coracobrachialis, epitrochlearis, tensor fasciae latae, and presemimembranosus. Relatively large size of stylohyoideus. Relatively more nearly equal size of the four parts of the pectoralis. No direct origin of rhomboideus from skull. Large area of insertion of cleidomastoideus. Origin of gracilis and sartorius by fleshy fibers. Tendinous insertion of gracilis. Lack of caudal head of semitendinosus. Longus colli extending posteriorly only to fifth thoracic vertebra.

So far as the musculature is concerned, *Mephitis* is the most primitive, at least the simplest, of the three forms here described and perhaps of all the mustelids whose musculature has been described. *Spilogale* is clearly a close relative of *Mephitis*, but it differs in several important respects as well as in many that can largely be correlated with its greater adaptability and agility. *Martes* displays the most specialized muscular system of the three, and judging purely from mechanical grounds is seemingly so constructed as to permit almost



the maximum of agility. The differences between *Martes* and *Spilogale* are greater than the differences between *Spilogale* and *Mephitis*. Collectively, and in most cases individually, the palaeotelic weight is regarded as greater than the weight of the differences found between *Spilogale* and *Mephitis*.

### LITERATURE CITED

CHATIN, M. J.

1874. Glandes odorantes des Mammifères (Carnassiers et Rongeurs). Ann. d. Sci. Nat., ser. 2, Zool. et Paleo., 19, 1-135, pls. 1-9.

REIGHARD, J., AND JENNINGS, H. S.

1901. Anatomy of the cat (ed. 2, revised; Henry Holt and Company), pp. i-xx, 1-498, 173 figs. in text.

WINDLE, B. C. A., AND PARSONS, F. G.

- 1897-1898. On the anatomy of the terrestrial Carnivora. Proc. Zool. Soc. London, 1897, 370-409; 1898, 152-186, 17 figs. in text.

*Transmitted April 26, 1926.*





SYSTEMATIC NOTES ON THE  
SUBSPECIES OF *BASSARISCUS ASTUTUS*  
WITH DESCRIPTION OF ONE NEW  
FORM FROM CALIFORNIA

BY

E. RAYMOND HALL.

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Vol. 30, No. 3, pp. 39-50, plates 2 and 3

Issued September 8, 1926

· UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# SYSTEMATIC NOTES ON THE SUBSPECIES OF *BASSARISCUS ASTUTUS* WITH DESCRIPTION OF ONE NEW FORM FROM CALIFORNIA

BY  
E. RAYMOND HALL

(Contribution from the University of California Museum of Vertebrate Zoology)

---

Examination of the material in the Museum of Vertebrate Zoology representing the genus *Bassariscus* revealed a specimen from Escondido, California, that differed so markedly from other specimens in the collection as to suggest the existence of an unnamed race in southern California. Additional material loaned from the collection of Mr. Donald R. Dickey showed this to be the case. Through the courtesy of Dr. Alexander Wetmore, Mr. Gerrit S. Miller, Jr., and Dr. Edward W. Nelson, certain especially pertinent specimens, for example, Baird's type of *Bassariscus raptor*, from the collections of the United States National Museum and the Biological Survey have also been examined. Acknowledgments are also made to Mr. Joseph Mailliard and Miss Mary E. McLellan, of the California Academy of Sciences, and Mr. Charles D. Bunker, of the University of Kansas, for the use of material in the collections under their charge.

In all, the following examples of the *Bassariscus astutus* group have been examined: *B. a. flavus*, 3 skulls-only and 3 skulls with skins; *B. a. nevadensis*, 2 skulls with skins; *B. a. saxicola*, 2 skulls-only and 1 skin-only; *B. a. palmarius*, 2 skulls with skins; *B. a. raptor*, 24 skulls with skins, 4 skulls-only, and 5 skins-only; and 5 skulls with skins of the new race from southern California which may be known as

## ***Bassariscus astutus octavus*, new subspecies**

*Type*.—Male, old adult, skull and skin; no. 27860, Mus. Vert. Zool.; San Luis Rey River, 1700 feet altitude, near Escondido, San Diego County, California; obtained by James B. Dixon March 6, 1925; sent alive to Joseph Dixon and prepared by him March 27, 1925; original number 6624, J.D.

*Diagnosis*.—A *Bassariscus* of the species *astutus*. Size as in *Bassariscus astutus raptor*. Color: no black on legs, feet, or ears; upper surface of forefoot nearly white, about cartridge buff (of

TABLE 1  
MEASUREMENTS (in millimeters) of *Bassariscus* FROM CALIFORNIA. All are old males of nearly equal age.

| Museum   | Catalogue number                               | Locality   | Total length             | Tail                     | Hind foot            | Basilar length                               | Breadth of rostrum between median margins of infraorbital foramina | Breadth of rostrum measured between Pm1 and Pm2 | Greatest breadth across upper tooth rows (between outer borders of first upper molars) | Zygomatic breadth                            | Maxillary breadth                            |
|--|--|--|--------------------------|--------------------------|----------------------|--|--|---|--|--|--|
| Mus. Vert. Zool.<br>D. R. Dickey   | 27860<br>G75                                   | <i>Bassariscus astutus octavus</i><br>Escondido, San Diego Co.<br>San Antonio Cañon, Los Angeles Co  | 775<br>740               | 400<br>370               | 73<br>64             | 70 2<br>70 5                                 | 16 6<br>16 5   | 13 2<br>13 2                                    | 22 1<br>22 9   | 48 0<br>46 8                                 | 34 5<br>33 4                                 |
| U. S. Nat. Mus.<br>Calif. Acad. Sci.<br>Mus. Vert. Zool.<br>Mus. Vert. Zool.<br>Mus. Vert. Zool.<br>Mus. Vert. Zool. | 976<br>708<br>34305<br>34306<br>23892<br>21561 | <i>Bassariscus astutus raptor</i><br>Santa Rosa, Sonoma Co.<br>Paine Creek, Tehama Co.<br>Paine Creek, Tehama Co.<br>Hetch Hetchy Valley, Tuolumne Co<br>El Portal, Mariposa Co. | 811<br>773<br>770<br>737 | 419<br>390<br>380<br>369 | 78<br>70<br>65<br>70 | 75 0<br>72 8<br>72 4<br>72 9<br>72 9<br>71 0 | 18 2<br>17 0<br>17 0<br>17 5<br>17 7<br>18 0                       | 15 0<br>13 5<br>13 5<br>14 1<br>13 4<br>14 5    | 25 0<br>24 0<br>24 8<br>24 4<br>24 3<br>24 7   | 52 ±<br>51 2<br>52 0<br>50 8<br>49 6<br>50 2 | 35 +<br>34 7<br>33 8<br>35 4<br>35 2<br>34 0 |

Ridgway, 1912); relative extent of white bands on tail greater than in *raptor*; proximal three dark bands on tail tinged with buff; neck and top of head near smoke gray; a general reduction of black and lighter tint of buff as compared with *raptor*. Cranium: antero-internal angle of tympanic bulla more inflated than in *raptor*; brain case not more inflated than in *raptor*; rostral region narrow; width across palate (measured from lateral borders of first upper molars) less than 23 mm.; upper tooth rows straighter than in *raptor* or than in any other form examined. (See table 1 for measurements.)

*Distribution*.—Represented in Upper Sonoran Zone of San Diego, eastern San Bernardino, Los Angeles, and Ventura counties, California.

*Specimens examined*.—Total number 5, from following localities in California: Escondido, San Diego County, 1; Mill Creek Cañon, San Bernardino County, 1; San Antonio Cañon, Los Angeles County, 1; Matilija, Ventura County, 2.

*Remarks*.—No. 33551, Mus. Vert. Zool., a young individual from San Bernardino County, is typical in that it agrees with the type. No. G75, collection of Donald R. Dickey, differs only in being slightly darker on the back; but even in this respect it is referable to *octavus* rather than to *raptor*. The two specimens, nos. 3957 and 3958, Mus. Vert. Zool., from Matilija, Ventura County, are, however, intermediate between *octavus* and *raptor*. Except for the absence of black on the feet and the relatively large extent of the white caudal rings they could be assigned to one race as easily as to the other. On the basis of cranial characters, one specimen is referable to *raptor* and the other to *octavus*, although neither is a typical representative. With the exception of the larger of these two specimens, no. 3958, all specimens of *octavus* measure less than 23 mm. across (outside dimensions) the first upper molars or fourth upper premolars. Without exception every specimen of the large series of *raptor*, which includes various ages of both sexes, has the corresponding dimension greater than 23 mm.

The color characters of the new form are fully as striking, if not more so, as the cranial characters, but call for no comment except that the general pallor is a type of coloration commonly found in mammals and birds of the San Diegan faunal district as compared with related forms occurring in more northwestern faunal districts.

The name *raptor* demands special consideration in the present case since the type locality of this form appears never to have been determined.

Baird's original description (1859, p. 19) and comments, here given in full, on the specimen designated by him as the type are as follows:

In the spring of 1852 (April 23) a specimen of *Bassariscus* was killed in a hen-roost, near Washington, after it had committed great devastation among the poultry of the neighborhood. It had evidently escaped from confinement, as shown by the marks of a collar around the neck. There was, of course, no indication whence it came originally, but it was supposed to have been brought from California. This specimen is somewhat different from those obtained in Mexico and Texas, although perhaps not specifically distinct. The tail is strikingly different in having the black rings fewer in number and of much



greater extent compared with the white portion. Of these black rings there are only five distinctly marked ones besides the tip, and the last or sub-terminal one is more than two inches long instead of about one. Below, the black ring is nearly complete, separated only for the thickness of the vertebrae by the white of the under surface. There is no appreciable difference in the colors of the remaining portions of the body. The ears are decidedly smaller. Very considerable differences are discernible between the skull of this specimen and others; the cranium is broader, but more constricted behind the orbital processes of the frontal bone; the distance between the zygomata is considerably greater, and the temporal crests of opposite side much closer together. The pterygoid bones, also, are further apart. The proportion of greatest breadth of skull to length is as 63 to 100 instead of 59, as in No. 4, from Texas. Should the examination of further specimens show these distinctions to be such as to indicate a different species, it might be called *Bassaris raptor*.

Allen (1879, p. 333) states:

In passing, I may add that the examination of more material shows that the cranial differences here indicated are not important, and show mainly only the usual variations accompanying differences of age in *Bassaris astuta*. The color of the tail very nearly coincides with that of a specimen before me from Oregon, with which it so much more nearly agrees than with Texas examples that I have little doubt that the supposed Californian origin of *Bassaris raptor* is its correct locality. The wide separation of the pterygoid bones is certainly exceptional, but is probably strictly individual, as I find a perfectly parallel variation in this highly variable feature in the skulls of *B. sumichrasti*. Consequently in *Bassaris raptor* we have the earliest synonym of *B. astuta*.

Rhoads (1893, p. 414) in discussing a specimen from Oregon remarks that:

Should the Oregon specimen here described prove to indicate the average condition of the species along the Pacific coast to the northward, as seems probable, the form there prevailing may require to be varietically distinguished under the name *raptor* Baird, this name doubtless referring to the Pacific coast form as already explained.

On page 415 (*loc. cit.*), Rhoads points out that:

In either case the question arises as to the tenability of the name '*raptor*' for the northern form. It was originally proposed for a Pacific Coast species.

The value of the name is, in the first place, lessened by the fact that it was applied to an animal escaped from confinement in the east and "supposed" to come from California.

In the last paragraph on page 415, in discussing the characters Baird claimed for *raptor*, Rhoads notes that: "Dr. Allen has shown, and the series in my possession verifies his view, that these cranial differences are accountable to age, sex and individual variation." Finally (*loc. cit.*, p. 416), he states: "Should the so-called *astutus* of the United States and northern Mexico prove a distinct species, the small, dark coast form from northern California northward (not of

central and southern California) should be made a sub-species of *flavus*. In that case it should be called *Bassariscus flavus oregonus*." In a footnote the type is designated as no. 1614, Collection of the Academy of Natural Sciences of Philadelphia.

The "curious inconsistency," as Merriam (1897, p. 186) terms it, between the two statements of Rhoads (*loc. cit.*, pp. 414, 416) leaves the name *raptor* unassigned either as a tenable name or as a synonym of any race. Merriam (*loc. cit.*, pp. 186, 187) has the following to say regarding Baird's type:

I have compared both the skin and skull of this specimen with specimens from northern California and Oregon, and find that they agree closely in all respects, except the interpterygoid fossa, which is abnormally broad in the type specimen. The number and breadth of the black bands on the tail correspond with specimens from Oregon and northern California. The skull is a little larger than that of any Oregon specimen in the Department collection, but is almost exactly matched by a specimen from Glen Ellen, California. . . .

It is of course unfortunate that the type locality of Baird's specimen is not positively known, but Baird's repeated statement that it probably came from California was doubtless based on some information which he did not at the time care to publish; and the fact that the characters of the specimen, both external and cranial, agree with those of the northwest coast animal, leaves little doubt as to the general locality whence the animal came.

My own comparison of Baird's type with other available material convinces me, also, that it came from northern California. Although the fur is somewhat discolored, presumably from having been preserved in alcohol for a time, it furnishes important evidence in the present case. In the degree of contrast between the dark back, lighter sides, and buffy mid-marginal belly markings, it is matched by northern Californian animals and is unlike any specimen examined from any other region. The size of the animal, also, at once distinguishes it from *nevadensis* and the Lower Californian races. The dark markings on the outside of the lower leg and foot distinguish it from *flavus*, *octavus*, and *palmarius*. The markings on the tail are matched only in several northern Californian specimens.

The cranium of the type of *raptor* agrees in size with crania from Texas and California. Thus its size is greater than in *nevadensis* or the Lower Californian races and, to judge from the measurements given by Rhoads (*loc. cit.*, p. 416), less than in *astutus* from Mexico. The wide palatal region and consequent bowed tooth rows distinguish it from *octavus*. The tooth rows are also more bowed than in any skulls seen of *flavus*. In all skulls of *flavus* examined the greatest width of the brain case comes at the junction of the squamosal and parietal directly above the external auditory meatus, whereas in nearly all

Californian specimens, and in Baird's type, the greatest width comes at the *lower* margin of the squamosal immediately above the external auditory meatus. The wide separation of the pterygoids in Baird's type is not equaled in any specimen seen of the several races of *astutus*. Apparently this is an extreme individual variation.

Any one of several of the above-mentioned characters that Baird's type and the northern Californian animals have in common and that at the same time distinguish them from specimens from all other areas is seemingly sufficient to establish the general region whence Baird's type came as northern California or possibly Oregon. With *all* the above cited characters there can be, it is believed, no question at all that specimen no. 97/976, United States National Museum, designated by Baird as type of *Bassariscus raptor*, came from northern California. .

No specimens from Oregon have been examined, but it is believed that Baird's type did not come from there because one specimen, no. BX7, collection of Donald R. Dickey, from Bridgeville, Humboldt County, California, and several specimens in the Museum of Vertebrate Zoology collection from Trinity County, California, are appreciably darker than the type of *raptor* and other specimens from farther south in California. Specimens from the Yosemite region of California average paler than the type of *raptor* and than specimens from the general region of Sonoma and Solano counties. The specimen which, in both cranial and external characters, most exactly matches the type of *raptor* is no. 708, ♂, old adult, from Santa Rosa, Sonoma County, California, in the collection of the California Academy of Sciences. Merriam (1897, p. 186), from a comparison of Baird's type with other Californian material not seen by me, also found the type specimen of *raptor* most nearly matched by a specimen from Sonoma County, in this case by one from Glen Ellen. In view of the foregoing stated facts I hereby designate, by restriction, Glen Ellen, Sonoma County, California, as the type locality of *Bassariscus astutus raptor* (Baird).

Accordingly, *Bassariscus astutus oregonus* Rhoads stands as a synonym of *B. a. raptor* (Baird), as Merriam (*loc. cit.*) and Grinnell (1913, p. 289) have previously so regarded it. It should be noted, however, that specimens from the extreme northern part of California are darker than those from farther south. Also, no. BX7 from Humboldt County, California, is unique in having much flattened tympanic bullae. Whether this represents the average condition of Oregon animals, whether it represents a distinct race in the Humboldt region, or whether it is merely individual variation, may be determined only with more material. In any event it is possible, but to

the writer seemingly improbable, considering the present standards limiting the amount of geographic variation properly recognizable by separate name, that specimens from Oregon represent a distinct race. In event this should prove to be the case the name *oregonus* will of course be available for this form, since Rhoads's type of *oregonus* is from Grants Pass, Josephine County, Oregon.

Intergradation has been assumed but in most cases never proved to exist between the several forms of *Bassariscus* inhabiting the United States, Lower California, and much of Mexico. In the material before me are the two previously mentioned specimens from Matilija, California, which do show intergradation between *octavus* and *raptor*. Several specimens from Mariposa County, California, are grayer than those from any other part of the State and in color suggest intergradation of *raptor* with *nevadensis* as represented by two specimens in the Museum of Vertebrate Zoology from Roosevelt, Arizona. However, in general size and cranial characters the specimens from Mariposa County show little if any tendency toward *nevadensis*. Two specimens, nos. 6957 and 6938, collection of Donald R. Dickey, from 14 miles east of Fort Lowell, Arizona, although in coloration much more nearly like *flavus* than like *nevadensis*, are intermediate between these two forms. *B. a. flavus*, as represented by no. 1268 from Waco, Texas, no. 4865 from Valverde County, Texas, no. 4866 from Atascosa County, Texas, and no. 4867 from Bexar County, Texas, all in the collection of the Kansas University Museum, is larger than the Fort Lowell animal, whereas *nevadensis* is smaller than the Fort Lowell animal. These Fort Lowell specimens are intermediate between the two last-named races in cranial characters, too, but also possess certain cranial characters not seen in either *flavus* or *nevadensis*. It is possible that these two specimens represent a recognizable race. Material from New Mexico, which I do not have, would probably decide this point. In any event, they are intermediate in several respects and provide strong indication of intergradation between *nevadensis* and *flavus*.

Whether or not *palmarius*, the one described mainland form from Lower California, intergrades with *octavus* is not known. In the course of field work for the Museum of Vertebrate Zoology in Lower California, Mr. Chester C. Lamb learned that a ring-tailed cat had been taken by a local resident at Concepcion, latitude 31°, altitude 6000 feet, Sierra San Pedro Martir, Nelson (1921, p. 33) records *bassarisks* as occurring at San Ignacio, Lower California, which is about 20 miles north of latitude 27°. Thus ring-tailed cats do occur in at least part of the territory between Comondu, Lower California, the type locality

of *palmarius*, and Escondido, California, the type locality of *octavus*, and it seems probable that there is intergradation between the two races.

Of the two insular forms of this group, *saxicola* and *insulicola*, the latter appears never to have been treated in the literature as other than a subspecies of *astutus*. On the other hand, *saxicola* was described (see Merriam, 1897, p. 185) as a distinct species and seems to have been so regarded by most subsequent writers. Nelson (1921, p. 128), however, treats *saxicola* as a subspecies of *astutus*. Seemingly a useful, although perhaps not a universally applicable, criterion for the treatment of insular forms is the consideration, that if, in the mainland forms, where intergradation does occur, greater differences exist than exist between the insular form and a nearby mainland form, the insular form should be treated as a subspecies. In short, the criterion is degree of difference, with the limitation of geographic adjacency, rather than intergradation. Although, upon comparison of material, I find the distinguishing characters of *saxicola* as pointed out by Merriam to be considerable, I follow Nelson in treating it as a subspecies of *astutus* since, to judge from Rhoads's description and measurements (*loc. cit.*, p. 416) of *B. a. astutus*, it and *B. a. palmarius* differ more from each other than do *palmarius* and *saxicola*.

The several races of *Bassariscus astutus*, with their type localities, may now stand as follows:

*Bassariscus astutus astutus* (Lichtenstein). Southern Mexico, exact locality unknown.

*Bassariscus astutus flavus* Rhoads. Texas, exact locality unknown.

*Bassariscus astutus octavus* Hall. Escondido, San Diego County, California.

*Bassariscus astutus raptor* (Baird). Glen Ellen, Sonoma County, California (by restriction).

*Bassariscus astutus nevadensis* Miller. Eldorado Cañon, Clark County, Nevada.

*Bassariscus astutus palmarius* Nelson and Goldman. Comondu, Lower California, Mexico.

*Bassariscus astutus insulicola* Nelson and Goldman. San José Island, Gulf of California, Lower California, Mexico.

*Bassariscus astutus saxicola* C. H. Merriam. Espiritu Santo Island, Gulf of California, Lower California, Mexico.

## LITERATURE CITED

ALLEN, J. A.

1879. On the species of the genus *Bassariscus*. Dept. Interior, Bull. U. S. Geol. and Geog. Surv., 5, 331-340.

BAIRD, S. F.

1859. Special report upon the mammals of the Mexican boundary. Washington, D. C., 1-55.

HOLLISTER, N.

1917. Some effects of environment and habit on captive lions. Proc. U. S. Nat. Mus., 53, 177-193, pls. 22-25.

MERRIAM, C. H.

1897. Description of a new *Bassariscus* from Lower California, with remarks on '*Bassariscus raptor*' Baird. Proc. Biol. Soc. Washington, 11, 185-187.

GRINNELL, J.

1913. A distributional list of the mammals of California. Proc. Calif. Acad. Sci., ser. 4, 3, 265-390, pls. 15, 16.

NELSON, E. W.

1921. Lower California and its natural resources. Nat. Acad. Sci., Memoir, 16, 1-194, pls. 1-34, 1 map.

RHOADS, S. N.

1894. Geographic variation in *Bassariscus astutus*, with description of a new subspecies. Proc. Acad. Nat. Sci. Phila., 1893, 413-418.

*Transmitted July 26, 1926.* .

## EXPLANATION OF PLATES

### PLATE 2

Dorsal views of crania of ring-tailed cats. All natural size.

Photographs retouched.

*a*, *Bassariscus astutus octavus*; type, no. 27860, Mus. Vert. Zool.; ♂; Escondido, San Diego County, California.

*b*, *Bassariscus astutus octavus*; no. G75, collection of Donald R. Dickey; ♂; San Antonio Cañon, Los Angeles County, California.

*c*, *Bassariscus astutus raptor*; type, no. 97/976, U. S. Nat. Mus.; undoubtedly a male; Washington, D. C. (escaped from captivity).

*d*, *Bassariscus astutus raptor*; no. 708, Calif. Acad. Sci.; ♂; Santa Rosa, Sonoma County, California.

The example of *raptor* shown in figure *d* is the one of all specimens examined which most nearly matches Baird's type, shown in figure *c*.

*a*



*b*



*d*



### PLATE 3

Ventral views of crania of ring-tailed cats. All natural size.

Photographs retouched.

*a*, *Bassariscus astutus octavus*; type, no. 27860, Mus. Vert. Zool.; ♂; Escondido, San Diego County, California.

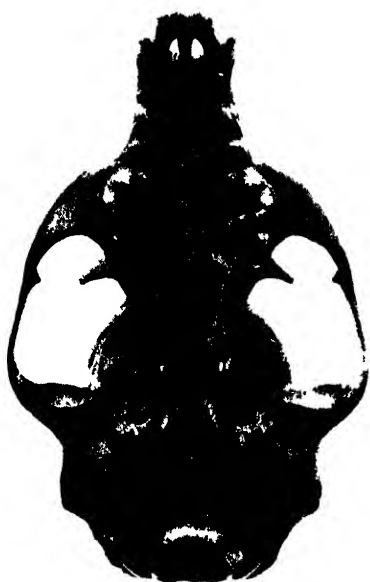
*b*, *Bassariscus astutus octavus*; no. G75, collection of Donald R. Dickey; ♂; San Antonio Cañon, Los Angeles County, California.

*c*, *Bassariscus astutus raptor*; type, no. 97/976, U. S. Nat. Mus.; undoubtedly a male; Washington, D. C. (escaped from captivity).

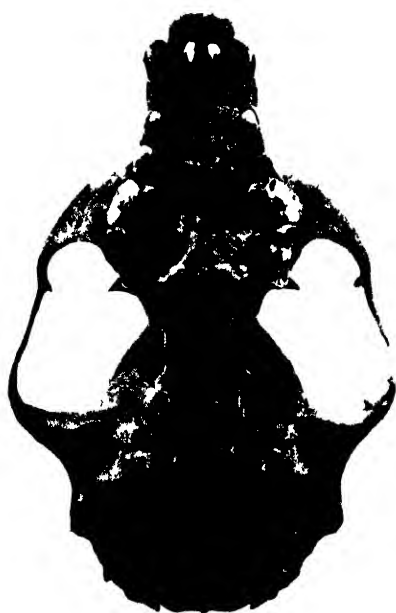
*d*, *Bassariscus astutus raptor*; no. 708, Calif. Acad. Sci.; ♂; Santa Rosa, Sonoma County, California.

The narrow palatal region of *octavus* may be noted by comparison of figures *a* and *b* with *c* and *d*. The great width of the interpterygoid fossa in the type of *raptor* is readily appreciable upon comparison of figure *c* with *a*, *b*, and *d*. Of the four old specimens here shown, Baird's type is seemingly the oldest. As indication of its advanced age, note the worn condition of the teeth and the strong, rugose points of muscle attachment in figure *c*, of both plates 2 and 3. The rounded zygomatic arch of Baird's type, which is better seen in an oblique view from above, in contrast with the flat zygomatic arches of other males of equal age, is here shown, at least near the base of the squamosal root of the arch. In the light of the cranial differences found by Hollister (1917, p. 185) between park-reared and wild killed lions, wolves, etc., this specimen of *Bassariscus* might also be regarded as having been in captivity for a considerable period of time.

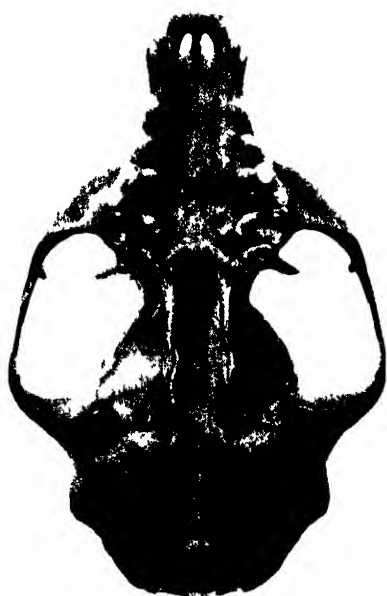
*a*



*b*



*c*



*d*



REPORT ON A COLLECTION OF BIRDS AND  
MAMMALS FROM THE ATLIN REGION,  
NORTHERN BRITISH COLUMBIA

BY

HARRY S. SWARTH

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 4, pp. 51-162, plates 4-8, 11 figures in text  
Issued September 24, 1926

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND





Young (in the foreground) and adult (in the distance) of the golden-crowned sparrow (*Zonotrichia coronata*), shown in the surroundings frequented by the species in northern British Columbia. Inset, egg of the golden-crowned sparrow, natural size.

# REPORT ON A COLLECTION OF BIRDS AND MAMMALS FROM THE ATLIN REGION, NORTHERN BRITISH COLUMBIA

BY

HARRY S. SWARTH

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

## CONTENTS

|   | PAGE |
|---|------|
| Introduction                                  | 51   |
| Itinerary and descriptions of localities      | 53   |
| Zonal and faunal position of the Atlin region | 56   |
| Check list of the birds                       | 59   |
| General accounts of the birds                 | 61   |
| Check list of the mammals                     | 145  |
| General accounts of the mammals               | 146  |
| Literature cited                              | 152  |

## INTRODUCTION

During the summer of 1924 the Museum of Vertebrate Zoology sent an expedition into the Atlin region, in extreme northwestern British Columbia. The expenses of this expedition, as of all previous zoological work carried on in the northwest by this Museum, were defrayed by Miss Annie M. Alexander, whose interest in the Museum's work, and particularly in developing a knowledge of the vertebrate natural history of the northwest, has been unflagging. Atlin was chosen as a base largely on account of its geographical position with relation to the valleys of the Stikine and Skeena rivers, to the southward, which had been visited by Museum parties in previous years.

The writer went alone from the Museum, that is, unaccompanied by any Museum assistant, but he was fortunate in being joined at the outset by Major Allan Brooks, of Okanagan Landing, British Columbia. Major Brooks painted and collected specimens independently, but the companionship proved mutually helpful in many ways. Specimens collected by the writer consist of 387 birds, 76 mammals, 12 amphibians, 11 birds' nests, and 16 sets of birds' eggs. Major Brooks' collection of birds was also at my disposal in writing the report that follows.



Acknowledgments are due to the Dominion Parks Branch, Department of the Interior, Canada, for permission to collect migratory birds, and to the Game Conservation Board, Vancouver, for permission to collect non-migratory birds and for other courtesies.

In working up the collection it proved necessary to borrow specimens from many institutions. The study of the ptarmigans in particular called for the assemblage of as large series of certain forms as could be brought together, and appeal was made to all museums and private collections that seemed likely to have pertinent material. Generous response to the many requests for the loan of specimens came from all who were asked, comprising the following: American Museum of Natural History, New York (including many specimens from the Sanford collection); Carnegie Museum, Pittsburgh; Colorado Museum of Natural History, Denver; Museum of Comparative Zoology, Cambridge; Museum of History, Science and Art, Los Angeles; Provincial Museum, Victoria; United States Biological Survey; United States National Museum; Victoria Memorial Museum, Ottawa; Louis B. Bishop; Donald R. Dickey; George Willett.

To Major Brooks I am indebted for help extended daily during the season's field work, for specimens turned over to me from day to day, field observations proffered, and for advice and critical comments pertaining to the systematic treatment of various species. The cordial assistance extended to us both by individuals resident in Atlin, whose acquaintance we made there, was a most important factor in making our work pleasant and profitable. In particular, mention should be made of Mr. C. L. Monroe, Government agent, for aid in his official capacity, and, together with Mrs. Monroe, for many unofficial courtesies; of Mr. A. B. Taylor, Government telegraph operator, a sportsman and a keen observer, in whose company I made many pleasant trips, who aided in securing numerous specimens and who, with Mrs. Taylor, did all he could to make our summer a pleasant one; and of Mr. H. Maluin, whose cordial welcome to his mining camp on Otter Creek enabled us to work in that region. On the train, en route from Skagway, we first made the acquaintance of Inspector Moorhead, of the Royal Canadian Mounted Police, who, then and later in the summer, lost no opportunity of extending such courtesies as lay in his power. To Corporal Robert McCleery and Mrs. McCleery, in their isolated post on Lake Teslin, the writer is indebted for cordial hospitality and for aid in securing needed specimens. From Mr. and Mrs. John Garrett, of Atlin, we received innumerable courtesies.

The drawings of birds' bills and tails illustrating parts of this report were made by Miss Anna Hamilton. The outline maps illustrating birds' ranges are the work of Miss Margaret W. Wythe, of the Museum staff.

In September, 1913, and from June 5 to August 19, 1914, the Provincial Museum, Victoria, British Columbia, carried on field work in the Atlin region. The first trip was conducted by Mr. F. Kermode, Director, with Mr. E. M. Anderson as assistant, the second by Mr. Anderson and Mr. C. B. Garrett, and both were reported upon in annual reports of the Provincial Museum for the years 1913 and 1914, respectively. We found these published accounts of the birds and mammals that were collected extremely useful, and had occasion to refer to them constantly during our season's work.

## ITINERARY AND DESCRIPTIONS OF LOCALITIES

I was joined by Major Brooks at Vancouver the morning of May 17. We left Vancouver that evening, arrived at Skagway, Alaska, early in the morning of May 21, and at Carcross, Yukon Territory, the afternoon of the same day. We had planned to go on at once to Atlin, but navigation had not yet opened on the lakes, and we therefore remained at Carcross for one week. On May 27 we took advantage of an opportunity to reach Atlin on a motor boat that was taking the mail, the first to be forwarded to that place for many weeks. We left Carcross at 1 P.M., reached the portage at Taku about midnight, and Atlin, across the lake, two hours later.

The town of Atlin remained our base throughout the summer, the only long departure therefrom being to a camp in lower Otter Creek, where we stayed from July 26 to August 9. Major Brooks left on August 30, for a brief stay at Log Cabin, White Pass, en route homeward. I left Atlin on September 24, reaching Berkeley on October 3.

On September 7, at the invitation of Captain Moorhead, Mr. Monroe, and Mr. Taylor, I accompanied them on a trip to the police post at Nisutlin Bay, Teslin Lake, some eighty miles (by the trail) northwest of Atlin. The first day we traversed the length of Surprise Lake and then the trail to Gladys Lake, twelve miles beyond. The second day was spent at that point (fortunately in comfortable quarters) in a downpour of rain that lasted the whole day long. The third evening we reached Grouse Creek, and the fourth afternoon

Teslin Lake. We left Teslin on the return trip the morning of September 13, reaching Atlin September 15. The trail lies in the lowlands the whole distance, passing through stretches of spruce, pine, and poplar woods at intervals, with occasional tracts of open meadow and marsh land. Rugged mountains enclose Surprise Lake, but beyond that point, to the northeast, the mountains are left behind and rolling, forested country stretches in all directions, save for isolated groups of peaks such as the conspicuous Dawson Peaks (locally known as the Four Aces) on the British Columbia-Yukon boundary at Lake Teslin.

#### CARCROSS

This is the Caribou Crossing of former days, now a station on the White Pass and Yukon Railroad. It is situated at the junction of Bennett and Tagish lakes, near the north base of White Pass, sixty-eight miles inland from Skagway. Our limited work here was within a radius of six or eight miles of the town, and entirely in the lowlands, as the nearby mountains were inaccessible from the depth of soft, melting snow with which they were then covered. The valley is clothed with open woods, poplars and small jack pine mostly, interspersed with stands of white spruce, and with willow copses in the more swampy ground. A large slough (with wide margins of exposed mud in May, filled with water in September) lies but a short distance from the town, an attraction for water birds of many sorts. A striking feature of this region is the vast expanse of shifting sand dune country. The lower end of Lake Bennett is broadly margined with sand dunes, and as far as we went in the woods to the northward we found similar sandy mounds covered with forest trees. It is a windy region; during our stay there were strong winds daily rushing inland through the White Pass. (For a detailed discussion of the faunistic features of the region, see Osgood, 1900, pp. 8-12.)

#### ATLIN

The town of Atlin is on the east shore of Lake Atlin, at an altitude of 2200 feet. The valley bordering the east side of the lake is forest covered mostly, but the woods are open and easily traversed. Quaking aspen, or "poplar," is the dominant deciduous tree, and almost unbroken stands of poplar cover miles of territory. White spruce grows in many places in the lowlands, and in denser stands and over greater areas on the adjoining mountain sides. The lowland woods are broken

in many places by tracts of swamp, grass-covered or grown up with willow thickets, and the woods are interspersed with many small lakes. Three or four miles east of Atlin, Lake Como, the largest of these small lakes near the town, supports a considerable population of water birds.

Some four miles south of Atlin, Monarch Mountain rises (see pl. 6, fig. 5), the nearest peak of a series of rounded and, for the most part, not particularly rugged mountains, that border Pine Creek Valley to the eastward of Atlin and the lake shore to the southward. Conditions on this mountain may be briefly described, as generally applicable to that type of country in this region. Poplar woods border the lowest slopes of the mountain, but ascend its sides only a few hundred feet before giving way to the belt of darker and denser spruce. Between 3500 and 4000 feet altitude spruce is largely replaced by balsam fir, growing to large size at its lowest level and persisting over the summit of the peak in more or less dwarfed and prostrate form. At the upper edge of the spruce belt the woods become more thin, and are cleft by wider and wider areas of open grass or lupine covered slopes. On the summit (3800 to 5000 feet altitude) upright timber of any size disappears, save in a few sheltered spots, and the scattered thickets of scrubby balsam sprawling close to earth are surrounded by wide areas of open ground, grass covered or here and there grown up with false heather over limited damp areas. Creeping birch grows here, too, and in extensive tracts; on this particular mountain I saw little that was more than knee-high.

Directly opposite the town of Atlin lies a group of three islands, the nearest within a quarter of a mile from the shore, and none of them more than a few acres in extent (see pl. 5, fig. 2). A striking feature of these islands is the fact that of the forest trees with which they are covered nearly all are balsam fir. There are relatively few spruce or jack pine. On the adjacent mainland I saw no balsam at the lake level. The islands are the nesting grounds of small colonies of water birds (short-billed gull, Bonaparte gull, and Arctic tern) and they harbor an extraordinary number of small land birds. We listed fifteen species of land birds as nesting there, some of them (such as the black-poll warbler) extremely scarce on the neighboring mainland. These small birds, too, were rearing their young successfully, in contrast to conditions on the mainland, where subsequent destruction of nest, eggs, or young was the usual fate of most of the nests we found. On the islands there were no red squirrels, no chipmunks, and no

Canada jays; the absence of these factors may have been the favorable feature of the place. The nesting species of gulls and tern were not so fortunate, for they suffered severely from the raids of herring gulls, to the ultimate destruction of nearly all the young that were hatched.

#### OTTER CREEK

The upper portion of Otter Creek (3500 to 4000 feet altitude), where we worked for two weeks, may be described as characteristic of vast areas throughout this region that lie in an intermediate position between the wooded lowlands such as border Lake Atlin and the timberless mountain tops. Willow is the dominant forest growth along the bottom of this valley, never as large trees but as densely, growing, rounded bushes, rarely more than twenty feet high and usually much lower. On Otter Creek, as on some other streams, the necessities of hydraulic mining have caused the damming of the stream far up the valley. For miles above the lake thus formed the valley floor is transformed into a willow swamp, a haven for ducks.

The mountain slopes on either side, and much of the valley floor in the upper reaches of the stream, are dry and more sparsely covered with vegetation. There are extensive grassy areas, and at about 3800 feet altitude the creeping birch begins to be conspicuous. Mostly this is a rather innocuous shrub, low-growing and easily walked over or avoided, but I found some sections (at about 4000 feet altitude) where it formed a chaparral on hill sides and ridges ten feet high or more and well-nigh impenetrable.

On the surrounding mountain sides, especially on north and east facing slopes, spruce, and above that, balsam, grow in small groves in some places, in solid stands for miles on favored exposures. On Spruce Mountain, forming the western boundary of Otter Creek Valley, this forest ceased abruptly between 4500 and 5000 feet altitude. Above that boundary grassy slopes and ridges prevail, with a very little false heather in places and a few scattered thickets of balsam.

#### ZONAL AND FAUNAL POSITION OF THE ATLIN REGION

Atlin occupies a position relative to the coast about the same as Telegraph Creek, in the Stikine Valley, and Hazelton, in the Skeena Valley, 150 miles and 375 miles to the southward, respectively. Both of these places I had visited in previous years (see Swarth, 1922, 1924), and comparisons between the regions naturally follow. Atlin Lake is at

an altitude of 2200 feet, compared with Telegraph Creek at 540 feet, and Hazelton at 973 feet, and this increase in elevation, together with the more northern location, has almost eliminated at Atlin certain Canadian Zone elements that are conspicuous at the more southern stations. The lowlands of the Atlin region, it seems to me, are Hudsonian Zone, with but a slight infiltration of Canadian Zone species. There is no definable zone between the lowlands (2200 feet altitude) and the Alpine-Arctic mountain tops, with timber line between 3500 and 4000 feet. The same species of plants, mammals, and birds, with few exceptions, range from timber line downward in suitable places throughout the valleys. The converse of this, however, is not true, of birds at least, for all species of birds that occur in the lowlands do not range upward to timber line. Then, a further exception must be made of three species of birds, *Dendragapus obscurus flemingi*, *Spizella monticola ochracea*, and *Lanius borealis*, the former two occupying in abundance, the latter in small numbers, types of country that are found in some places immediately below timber line (see pl. 6, fig. 4). However, making due allowance for the more decidedly Hudsonian character of higher altitudes, the general tone of the valleys, too, is of the Hudsonian Zone. This is exemplified in the extensive stands of white spruce with such accompanying bird species as the Alaska hermit thrush, Hudsonian chickadee, Canada jay, goshawk, and spruce grouse, all occurring in abundance.

In the upper Skeena Valley the Canadian Zone is dominant, as demonstrated by the presence of many elements over a vast expanse of country. In the upper Stikine Valley, while the Canadian Zone characterizes the region, there are fewer bird species represented and they occur over a relatively restricted area. In the lowlands of the Atlin region there is but the merest infiltration of Canadian Zone elements into prevailing Hudsonian Zone surroundings.

Lakes and streams in the Atlin region all find their way into the Arctic drainage, and here, too, in coming from the south, one first finds a few real Arctic birds. Among such may be mentioned the pair of black-throated loons we saw, apparently in two minds as to nesting in the region, the northern phalarope, apparently breeding at Carcross, the gyrfalcon, and the northern shrike.

Some comparisons can be made of the status of certain species of birds at Hazelton, Telegraph Creek, and Atlin. *Bubo virginianus lagophonus* is abundant at Hazelton. We secured no horned owls at Telegraph Creek, but at Atlin the breeding subspecies is the more northern form, *B. v. subarcticus*. *Dryobates villosus monticola* is abundant at

Hazelton and Telegraph Creek. At Atlin, hairy woodpeckers were all but absent, but the specimens secured were the northern *D. v. leucomelas*. *Dryobates pubescens leucurus* is common at Hazelton, we found no downy woodpecker at Telegraph Creek, and at Atlin the one specimen of this species that was taken proved to be the northern *D. p. nelsoni*. *Selasphorus rufus* is abundant at Hazelton, less common at Telegraph Creek, and decidedly rare at Atlin. *Carpodacus purpureus purpureus*, abundant at Hazelton, was rare at Telegraph Creek, and seen once at Atlin. *Vireosylva gilva swainsoni*, abundant at Hazelton and Telegraph Creek, was represented by one pair seen at Atlin. *Oporonis tolmiei*, abundant at Hazelton and Telegraph Creek, was doubtfully identified once at Atlin (June 24, 1924; not included in the following list). *Setophaga ruticilla*, abundant at Hazelton and but little less numerous at Telegraph Creek, was decidedly rare at Atlin. *Penthestes gambeli abbreviatus*, found in small numbers near Hazelton and Telegraph Creek, was seen once at Atlin. *Cypseloides niger borealis*, *Chaetura vauri*, *Melospiza melodia morphna*, and *Piranga ludoviciana*, are species that apparently all find their northern limit near Telegraph Creek, none being seen at Atlin.

The non-occurrence of any form of *Passerella* in the Atlin region is of interest. *P. iliaca altivagans* was found breeding in the vicinity of Hazelton but nowhere near Telegraph Creek. Its absence in the Atlin region, too, suggests that there is a wide gap between the breeding ranges of *P. i. iliaca* and *P. i. altivagans*, and thus that these forms may not really be so closely related as I had supposed (Swarth, 1920, p. 93), a belief founded largely upon the appearance of certain winter birds of intermediate character. *Altivagans* apparently occurs throughout a wide range of territory between the habitat of *P. i. schistacea*, of the Rocky Mountain and Great Basin regions, and of *P. i. fuliginosa*, of the coast, but it does not seem to range northward as far as the summer home of *P. i. iliaca*.

Faunally, Atlin may be considered as the extreme southern limit of the Yukon region. As regards birds there are many southern species that find their northern limit a short distance to the southward, and certain characteristic northern species that extend barely this far south. The Atlin avifauna is of the interior, purely. There is not a single distinctively coastal species that penetrates this distance inland, less than one hundred miles away from salt water.

## CHECK LIST OF THE BIRDS

1. *Colymbus holboellii* (Reinhardt)
2. *Colymbus auritus* Linnaeus
3. *Gavia immer* Brünnich
4. *Gavia pacifica* (Lawrence)
5. *Gavia stellata* (Pontoppidan)
6. *Stercorarius parasiticus* (Linnaeus)
7. *Larus argentatus* Pontoppidan
8. *Larus brachyrhynchus* Richardson
9. *Larus philadelphia* (Ord)
10. *Sterna paradisaea* Brünnich
11. *Mergus americanus* Cassin
12. *Mergus serrator* Linnaeus
13. *Lophodytes cucullatus* (Linnaeus)
14. *Anas platyrhynchos* Linnaeus
15. *Nettion carolinense* (Gmelin)
16. *Spatula clypeata* (Linnaeus)
17. *Dafla acuta tzitzihou* (Vieillot)
18. *Marila affinis* (Eyton)
19. *Glaucionetta islandica* (Gmelin)
20. *Charitonetta albeola* (Linnaeus)
21. *Histrionicus histrionicus pacificus* W. S. Brooks
22. *Oidemia deglandi dixonii* W. S. Brooks
23. *Oidemia perspicillata* (Linnaeus)
24. *Branta canadensis* (Linnaeus), subsp.?
25. *Lobipes lobatus* (Linnaeus)
26. *Gallinago delicata* (Ord)
27. *Pisobia maculata* (Vieillot)
28. *Pisobia bairdii* (Coues)
29. *Pisobia minutilla* (Vieillot)
30. *Ereunetes pusillus* (Linnaeus)
31. *Totanus flavipes* (Gmelin)
32. *Tringa solitaria* Wilson
33. *Heterosceles incanus* (Gmelin)
34. *Actitis macularia* (Linnaeus)
35. *Numenius hudsonicus* Latham
36. *Oxyechus vociferus* (Linnaeus)
37. *Charadrius semipalmatus* Bonaparte
38. *Aphriza virgata* (Gmelin)
39. *Dendragapus obscurus flemingi* Taverner
40. *Canachites canadensis osgoodi* Bishop
41. *Bonasa umbellus umbelloides* (Douglas)
42. *Lagopus lagopus albus* (Gmelin)
43. *Lagopus rupestris rupestris* (Gmelin)
44. *Lagopus leucurus leucurus* (Swainson)
45. *Circus hudsonius* (Linnaeus)
46. *Accipiter velox* (Wilson)
47. *Astur atricapillus atricapillus* (Wilson)
48. *Buteo borealis harlani* (Audubon)



49. *Aquila chrysaëtos* (Linnaeus)
50. *Haliaeetus leucocephalus alascanus* C. H. Townsend
51. *Falco rusticolus rusticolus* Linnaeus
52. *Falco peregrinus anatum* Bonaparte
53. *Falco columbarius suckleyi* Ridgway
54. *Cerchneis sparveria sparveria* (Linnaeus)
55. *Pandion haliaetus carolinensis* (Gmelin)
56. *Bubo virginianus subarcticus* Hoy
57. *Bubo virginianus lagophonus* Oberholser
58. *Surnia ulula caparoch* (Müller)
59. *Ceryle alcyon caurina* Grinnell
60. *Dryobates villosus leucomelas* (Boddaert)
61. *Dryobates pubescens nelsoni* Oberholser
62. *Picoides americanus fasciatus* Baird
63. *Colaptes auratus borealis* Ridgway
64. *Chordeiles virginianus virginianus* (Gmelin)
65. *Selasphorus rufus* (Gmelin)
66. *Sayornis sayus yukonensis* Bishop
67. *Nuttallornis borealis* (Swainson)
68. *Myiochanes richardsonii richardsonii* (Swainson)
69. *Empidonax traillii alnorum* Brewster
70. *Empidonax hammondii* (Xantus)
71. *Empidonax wrightii* Baird
72. *Otocoris alpestris arcticola* Oberholser
73. *Pica pica hudsonia* (Sabine)
74. *Perisoreus canadensis canadensis* (Linnaeus)
75. *Corvus corax principalis* Ridgway
76. *Euphagus carolinus* (Müller)
77. *Carpodacus purpureus purpureus* (Gmelin)
78. *Loxia leucoptera* Gmelin
79. *Spinus pinus* (Wilson)
80. *Calcarius lapponicus alascensis* Ridgway
81. *Passerculus sandwichensis alaudinus* Bonaparte
82. *Zonotrichia gambelii* (Nuttall)
83. *Zonotrichia coronata* (Pallas)
84. *Spizella monticola ochracea* Brewster
85. *Spizella passerina passerina* (Bechstein)
86. *Spizella taverneri* Swarth and Brooks
87. *Junco hyemalis connectens* Coues
88. *Melospiza lincolni lincolni* (Audubon)
89. *Petrochelidon lunifrons lunifrons* (Say)
90. *Hirundo erythrogaster* Boddaert
91. *Iridoprocne bicolor* (Vieillot)
92. *Tachycineta thalassina lepida* Mearns
93. *Riparia riparia* (Linnaeus)
94. *Bombcilla garrula pallidiceps* Reichenow
95. *Lanius borealis* Vieillot
96. *Vireosylva gilva swainsonii* (Baird)
97. *Vermivora celata celata* (Say)
98. *Vermivora celata orestera* Oberholser
99. *Vermivora peregrina* (Wilson)
100. *Dendroica aestiva aestiva* (Gmelin)

101. *Dendroica coronata hooveri* McGregor
102. *Dendroica striata* (J. R. Forster)
103. *Dendroica townsendi* (J. K. Townsend)
104. *Seiurus noveboracensis notabilis* Ridgway
105. *Geothlypis trichas occidentalis* Brewster
106. *Wilsonia pusilla pileolata* (Pallas)
107. *Setophaga ruticilla* (Linnaeus)
108. *Anthus rubescens* (Tunstall)
109. *Sitta canadensis* Linnaeus
110. *Penthestes atricapillus septentrionalis* (Harris)
111. *Penthestes gambeli abbreviatus* Grinnell
112. *Penthestes hudsonicus columbianus* (Rhoads)
113. *Regulus satrapa olivaceus* Baird
114. *Regulus calendula calendula* (Linnaeus)
115. *Myadestes townsendi* (Audubon)
116. *Hylocichla ustulata swainsoni* (Tschudi)
117. *Hylocichla guttata guttata* (Pallas)
118. *Hylocichla guttata pallasii* (Cabanis)
119. *Planesticus migratorius migratorius* (Linnaeus)
120. *Ixoreus naevius meruloides* (Swainson)
121. *Sialia currucoides* (Bechstein)

## GENERAL ACCOUNTS OF THE BIRDS

### ***Colymbus holboellii*** (Reinhardt). Holboell Grebe

Present during our entire stay in the region. Pairs were seen in various lakes, large and small; and early in June the curious courting antics were commonly observed. No nests were found, nor were any young birds seen.

### ***Colymbus auritus*** Linnaeus. Horned Grebe

A pair or more could be found on every lake, large or small. Seen at Carcross, May 22, and a single bird was noted near Atlin on September 21, my last day afield. Migrating in numbers during the second and third weeks in September.

On July 18 a nest was found in a small lake at the head of Cañon Creek, about 3500 feet altitude. The young birds had apparently but just hatched. They, with one parent, were occupying the nest when it was found, and the family, as observed from a distance, returned to it when I left. The nest was a circular mass of sodden grass floating amid a sparse growth of short, green grass, about three feet from the shore. It was somewhat hidden by a small willow overhanging from the adjacent bank.

***Gavia immer* Brünnich. Common Loon**

Seen on most of the lakes, and presumably nests in the region. No evidence of breeding was found, however, other than the presence of loons, some in pairs, throughout the summer.

***Gavia pacifica* (Lawrence). Pacific Loon**

Seen at Carcross, presumably migrating, on May 22. The presence of a pair of Pacific loons on a small lake a few miles north of Atlin, on June 23 and 24, led to the hope that they would nest there. A few days later, however, they were gone, and no others were seen.

***Gavia stellata* (Pontoppidan). Red-throated Loon**

Seen on but one occasion, a single bird on Lake Atlin on June 20.

***Stercorarius parasiticus* (Linnaeus). Parasitic Jaeger**

One seen in pursuit of a gull at Lake Teslin, September 11. The jaeger was at close enough range to permit observation of details of color and markings.

***Larus argentatus* Pontoppidan. Herring Gull**

A nesting colony of this species on an island in Atlin Lake has been described by Anderson (1915, p. 9). Herring gulls were seen commonly along the shore of Atlin Lake all through the summer, at Surprise Lake in August, and at Teslin Lake during the second week in September. Herring gulls raided certain breeding colonies of short-billed gulls, Bonaparte gulls, and Arctic terns near the town of Atlin, to such effect that only an extremely small proportion of the young of those species survived.

There is a published record of the occurrence of *Larus californicus* at Lake Atlin (Anderson, 1915, p. 9), based upon a specimen in the collection of the Provincial Museum, Victoria. I have examined this specimen, which proves to be, though a rather small individual, unquestionably *Larus argentatus*.

***Larus brachyrhynchus* Richardson. Short-billed Gull**

Seen at Carcross, May 22. A small nesting "colony," consisting of at least four pairs and perhaps seven or eight, was distributed over the three islands nearest the town of Atlin. Short-billed gulls were

seen continually in some numbers along the lake shore, and the species was probably nesting at various points. We did not discover the colony alluded to above until all young birds had left the nests. Due to the ravages of the herring gull, as seemed evident, eggs and young in this colony were destroyed until just one young bird remained. This lone survivor, with wing quills partly grown but not yet able to fly, was several times seen, swimming on the lake, dodging attacks from a herring gull, which persisted until the entire adult population of short-billed and Bonaparte gulls came to the rescue.

A short-billed gull's nest was discovered July 15 on the "middle island" opposite the town of Atlin. It was placed in the top of a small balsam fir (with which trees these islands are thickly covered), about fifteen feet from the ground, and not at all easy to see in the flattened tree-top where it was placed. The young had been gone for some days at least, and buried in the bottom of the nest, entirely covered and hidden, was an addled egg (no. 1978). One or two other nests were seen in similar situations.

Two specimens of short-billed gull were preserved, an adult male (no. 44628) taken June 15, and a young female (no. 44629) molting from down to first winter plumage, taken July 14.

### ***Larus philadelphia* (Ord). Bonaparte Gull**

Seen at Carcross, May 22. Two days later a pair of these birds had apparently preëmpted one end of a slough at the edge of the town, and they dived at our heads with loud outcries whenever we approached.

At Atlin, this species, like the short-billed gull, was nesting on the islands opposite the town, and, as with the larger species, the young had left the nests before we discovered this breeding ground. There were apparently ten or twelve pairs of Bonaparte gulls domiciled upon the islands, and, due again to the raiding herring gulls, from all these broods but three young birds reached an age when they could fly.

Several nests were found on the islands, which, without question, must have belonged to this species. They were frail affairs, not much larger than waxwings' nests, placed on widespreading side branches of balsam firs, near the tops of the trees, some fifteen or twenty feet from the ground. Just as is seen in the descriptions of Bonaparte gulls' nests given by the several authors that are quoted in Bent's (1921, p. 176) "Life Histories," they were suggestive of pigeons' nests more than anything else.

Bonaparte gulls were seen on all the small lakes of the region, and may have been nesting in such places, too, though we had no positive evidence to this effect. The species apparently left early in August; none was seen after the first week of this month.

One specimen was collected (no. 44630), a young bird, taken July 14, molting from the down to first winter plumage, and not yet able to fly.

***Sterna paradisaea* Brünnich. Arctic Tern**

Seen at Carcross, May 22, on Tagish Lake May 27, and at Atlin upon our arrival the next day. Nesting in some numbers (ten or twelve pairs at least) on the islands opposite Atlin, and certainly at other nearby points also, for the birds were seen constantly along the shore of Atlin Lake and about some of the smaller lakes. On the islands mentioned, none of the young survived the onslaughts of the herring gulls.

The species was last seen August 8. One specimen was collected (no. 44631), a young bird taken July 14, molting from the down to first winter plumage.

***Mergus americanus* Cassin. American Merganser**

A single male bird was seen at Carcross on May 24. The species was not otherwise observed during the summer.

***Mergus serrator* Linnaeus. Red-breasted Merganser**

Apparently rare. An adult male was seen on Atlin Lake, June 6. Several were seen on Surprise Lake, September 15, and one collected (no. 44632), a young bird, fully feathered as regards body plumage but not yet able to fly.

***Lophodytes cucullatus* (Linnaeus). Hooded Merganser**

An adult male, a single bird, seen on a pond near Atlin on June 17, and watched through binoculars for some time. This is perhaps the most northwestern point of record for the species. Great Slave Lake, its northernmost limit in the interior, is but a little farther north than Atlin.

***Anas platyrhynchos* Linnaeus. Mallard**

Seen at Carcross, May 22. There were probably a few scattered pairs breeding in the marshes about Atlin, but not many. Only an

occasional bird was encountered, and at long intervals, during the summer. Flocks were seen at Lake Teslin, September 11, and at Fat Creek (between Teslin and Gladys lakes) on September 13. On September 21, my last day afield, I saw two mallards near Atlin.

***Nettion carolinense* (Gmelin). Green-winged Teal**

Seen at Carcross, May 23. About Atlin, though not common, there were scattered pairs nesting in most of the marshes. More were seen in flooded bottom lands of the upper portion of Otter Creek than anywhere else. Flocks of nearly full-grown young were noted July 28, on Otter Creek, but on August 6, at the same point, a brood of downy young was seen that could have been hatched but a few days. The species apparently leaves early for the south, though such late-hatched young as were just mentioned must linger to a relatively late date. No green-winged teal were seen about Atlin after the middle of August.

***Spatula clypeata* (Linnaeus). Shoveller**

A single bird, a cripple, was seen by Brooks on a pond near Atlin on June 27. At Carcross we were shown a mounted shoveller that had been shot near that town. The rarity there of this species may be attested by the fact that this bird had been preserved as a curiosity. No one in the community knew what it was.

***Dafila acuta tzitzihua* (Vieillot). American Pintail**

Seen at Carcross, May 22. A fairly common species about Atlin during the summer, and especially abundant in the swampy upper reaches of Otter Creek. The first young were noted on June 23, when two newly hatched broods appeared on Lake Como.

I saw no pintails, definitely recognized as such, after the end of August.

***Marila affinis* (Eyton). Lesser Scaup Duck**

Scaups seen at Carcross, May 22, were presumably *M. affinis*. This was the most numerous breeding duck in the Atlin region, where hardly a pond could be found that did not harbor at least one scaup family. Nests were built in grassy swales or marshes adjoining open sheets of water. Early in June these ducks were in pairs, but by the third week of that month most of the drakes were congregated in flocks by themselves, sometimes three or four birds together, sometimes ten or twelve.

On June 23 three nests were found in one marsh. Two of these were about twenty feet apart, the other some two hundred yards away. The two closely adjoining nests when found held, respectively, two and four eggs, the other, eight. The nests with two and four eggs, on July 2 held, respectively, nine and ten.

The three nests were similarly placed, each in a tussock of long marsh grass, barely above the level of the water, and they were similarly built. Construction was of the slightest, the nest walls being formed largely of growing grass, and the bottom of the same sort of grass, some placed there but mostly consisting of the crushed vegetation that had been growing on the hummock. The upper rim of the nest wall was dry, but the lower two-thirds was sodden and the eggs were wet. There was no down in any of the nests. In each case the parent bird could slip off of her eggs directly into water deep enough to swim in, six or eight inches in depth, and, by narrow channels through the hummocks, she could reach an open pond nearby.

On July 7 many male scaups were seen that were assuming the eclipse plumage. Two drakes noted July 18 were mostly in eclipse, but were strong on the wing. On July 20 the first downy young appeared. On September 19, the last date on which I visited a suitable spot for this species, several small flocks were seen, perhaps twenty-five or thirty birds, all told.

Four specimens were collected (nos. 44633-44636), one adult male, one adult female, and two downy young.

### ***Glaucionetta islandica* (Gmelin). Barrow Golden-eye**

Present at Carcross when we arrived, May 22. One of the most abundant ducks about Atlin; nearly as numerous as the lesser scaup and of even more general distribution. The difference in habitats of the two species lay in the greater abundance of the golden-eye in the little mountain lakes at high altitudes. We found no nests, but the situation of some of the broods seen precluded the possibility of their having been hatched within cavities in trees. Many families were found on lakes above timber line, long distances from trees of sufficient size to afford sheltering holes.

The first young appeared July 3. This particular brood was kept under observation until August 13. Originally nine in number, it was reduced (cause unknown) to seven by July 7. On August 13, the flock consisted of six, plus the mother, and the young then were about three-

fourths the size of their parent. Small patches of pale-colored down on the sides of the head were all that remained of the young plumage. The young were as yet unable to fly.

On June 14 six adult males were seen together, first evidence of the impending departure of the drakes, and during the next few days southward flying flocks were noted over Lake Atlin and elsewhere. No old drakes were seen during the latter part of the summer. One shot on June 30 was beginning to molt into the eclipse plumage.

Golden-eyes were seen on Lake Teslin, September 11, and there were a few still on Lake Como on September 19.

Six specimens collected, the adult male mentioned above, and five downy young, from two broods of different ages (nos. 44637-44642).

***Charitonetta albeola* (Linnaeus). Buffle-head**

Seen at Carcross, May 22 and 24. Not otherwise observed.

***Histrionicus histrionicus pacificus* W. S. Brooks**

**Western Harlequin Duck**

Breeds in small numbers and at widely scattered intervals throughout the region, where the species generally passes by the name of "wood duck." Two were seen on Lake Atlin, June 20. On September 1 a brood was encountered at "Blue Cañon," and two were collected, an adult female and a young male (nos. 44643-44644). The female had finished the annual molt and the young were full grown. On September 7 a brood was seen in the rushing water of Consolation Creek, near Gladys Lake.

***Oidemia deglandi dixonii* W. S. Brooks. Dixon White-winged Scoter**

At Carcross, May 24 to 26, white-winged scoters were arriving in numbers from the coast. The flights occurred in the evenings, when flock after flock appeared from over the snowy mountain barrier to the westward. They circled about overhead, a few individuals uttering harsh quacks at infrequent intervals; some flocks dropped down to rest in the nearby lakes, while others, after many aerial evolutions, eventually speeded on farther into the interior.

In the Atlin region there was a colony of this species established at Lake Como, but we saw none during the summer on any of the smaller lakes. Just how many pairs nested could not be accurately determined,



but there were at least twenty or twenty-five adults of each sex settled there at the beginning of the nesting season, and eight or ten broods of ducklings appeared upon the lake later on.

On June 1, at Lake Como, the scoters were all in pairs, and they continued so until near the end of the month. On June 29 the first small flocks of males were seen leaving for the coast; some remained inland until near the end of the summer.

On July 20 the first brood of young was seen, others following within a few days. Broods counted consisted of eight or nine ducklings, but counts had to be made soon after hatching, for the broods quickly merged into loosely assembled flocks so that it was not long possible to keep track of separate families. Sometimes two or three adults were seen in attendance upon sixteen or twenty young, and once a single duck appeared leading thirty-two small ducklings across the lake. The young were very self-reliant, and sometimes six or eight would be found foraging independently, unattended by any old bird. Thus this colony of white-winged scoters led a markedly communistic existence, individuals, young and old, gathering together into larger or smaller groups as suited their convenience at the time. The scaups, too, had as little seeming regard for family ties, their habits in these matters being much the same as with the scoters.

Young scoters but a day or two old were seen diving expertly, making long stays below the surface. Old birds, carefully watched through binoculars, were frequently seen to make use of their wings as they dived, but this was not invariably the case. White-winged scoters to the number of twenty or more were still on Lake Como on September 19, the last day I visited the lake.

Four specimens were preserved, ducklings not more than two or three days old (nos. 44645-44648).

#### ***Oidemia perspicillata* (Linnaeus). Surf Scoter**

An adult male that was seen on Lake Atlin, opposite the town, on July 21 and on several days following, was the only surf scoter encountered during the summer.

#### ***Branta canadensis* (Linnaeus), subsp. ? Canada Goose**

Canada geese were migrating in some numbers at Gladys Lake, September 8, and they were abundant at certain points on Lake Teslin, September 10 to 13. A flock of about fifty passed over Atlin on

September 21. As these were the only migrating geese I saw there, though they were so abundant on the more eastern lakes mentioned above, it would seem that Atlin Lake is not on the most generally used migration route of this species.

**Lobipes lobatus** (Linnaeus). Northern Phalarope

A pair of northern phalaropes that were seen in a swamp several miles north of Carcross on May 23 were observed going through courting antics and then copulating, and were thus judged to be preparing to nest there.

The first south-bound migrant, a single bird still in summer plumage, was seen near Atlin on July 21; a flock of about thirty-five birds appeared on August 27. On September 1 single birds and groups of two and three were found scattered over various small lakes above timber line.

**Gallinago delicata** (Ord). Wilson Snipe

Seen at Carcross, May 22. Breeds in fair abundance in the Atlin region; there was probably a pair or two in every swamp of any size. From the town of Atlin the "bleating" of the snipe could be heard almost continuously during June and early in July. Frequently when awakening at night during the brief period of partial darkness at that season, I heard snipe circling about overhead. The "bleat" under such conditions was very suggestive of the call of the California screech owl.

The birds were often observed performing these aerial evolutions, and in practically all respects our observations bear out the descriptive comments of Kitchin, Dawson, and Hoffmann, as detailed by the last mentioned writer (Hoffmann, 1924, p. 175). This performance ceased abruptly the middle of July, the last "bleating" being heard on July 17. The birds are otherwise unobtrusive, and I saw none after that date.

**Pisobia maculata** (Vieillot). Pectoral Sandpiper

Seen on but one occasion, a single bird in a flock of lesser yellow-legs on June 4.

**Pisobia bairdii** (Coues). Baird Sandpiper

Seen at Carcross, May 22. Not otherwise observed.

**Pisobia minutilla** (Vieillot). Least Sandpiper

Seen at Carcross May 22. At Atlin the first south-bound migrants appeared June 29, when two single adults were seen at different points. One of the birds was performing the usual mating flight. A few days later small flocks began to drop in at intervals, continuing until August 27, when the last was seen.

**Ereunetes pusillus** (Linnaeus). Semipalmated Sandpiper

A single bird, a south-bound migrant, was collected at Atlin, July 17. This specimen (no. 44649) is an adult female, in which the annual molt has just begun. Two were seen at close range on the shore of Morley Bay, Lake Teslin, September 12.

**Totanus flavipes** (Gmelin). Yellow-legs

Present in some numbers at Carcross, May 22, and evidently then preparing to nest. The birds were in pairs and noisy and solicitous at any invasion of their territory. Some were going through the nuptial flight and "song," some perched on tree-tops scolded the intruder. About Atlin there were yellow-legs in nearly every lowland swamp. While the breeding birds were thus distributed in pairs over the country, there were also wandering flocks that appeared at intervals during June and July. These were evidently composed of non-breeding individuals.

We found no nest, but Brooks collected a newly hatched chick on June 17. The downy young had the faculty of remaining invisible, or nearly so, but when almost full grown they became conspicuous about the edges of the ponds, and were then indifferent to approach. By July 20 the yellow-legs had nearly all left for the south; the last birds were seen August 13 and 14.

Three specimens were collected by me, young nearly or quite full grown (nos. 44650-44652).

**Tringa solitaria** Wilson. Solitary Sandpiper

First seen at Carcross, May 25. Early in June the species was encountered not uncommonly about Atlin, and the birds seen had all the appearance of being upon their nesting grounds. Individuals were going through their courting flight and song overhead, and some were

settled at certain spots where they resented intrusion. Whatever the reason, these birds all disappeared before the end of June, and we had no evidence that any broods were hatched in that vicinity. The first fall migrant appeared on upper Otter Creek, July 27, and during the next ten days they were of daily occurrence. Last seen August 6.

Two specimens were collected (nos. 44653-44654), an adult male at Carcross, May 25, and an immature male on Otter Creek, July 27. From outward appearances these birds might be referred to two different subspecies, the first to the eastern form, *Tringa solitaria solitaria*, the other to the western, *T. s. cinnamomea*, but I am not satisfied that this division is justified. These two subspecies, at best, are but poorly defined. The latest monographer of the group (Ridgway, 1919, pp. 353, 358, 363) gives the distinguishing characters of the two as follows: *Tringa s. solitaria*. Size smaller. "Summer adults with upper parts much more distinctly spotted with white; young with spotting on upper parts white or grayish white; white bars on tail averaging wider; the middle pair of rectrices never wholly grayish brown."

*T. s. cinnamomea*. Size larger. "Summer adults with upper parts much less distinctly spotted with white; young with spotting of upper parts brownish buffy or cinnamomeus; white bars on tail averaging narrower, the middle pair of rectrices often (usually?) wholly deep grayish brown."

An additional character cited by Brewster (1890, p. 377) in his description of *Totanus solitarius cinnamomeus*, but not used by Ridgway, is the presence in *cinnamomeus* of more or less "freckling" at the inner base of the outermost primary.

Examination in the present connection of some forty-odd specimens of eastern and western birds revealed no more satisfactory mode of dividing them than by regard to the points of capture. Some eastern specimens (from Indiana and Pennsylvania) are smaller than any western birds, but others are well within the size limits of *cinnamomea*. Also, some western birds, taken in the fall and presumably immature, are more cinnamomeous in color of upper parts. As regards distinctness of spotting above, and character of tail markings, I found it impossible to make division by these features. Most (but not all) western birds show more or less of the "freckling" at the base of the primary, and it is not present in any eastern specimens at hand.

The several characters indicated are independently variable, so that a given specimen may, on the basis of one certain feature, seem

referable to the eastern subspecies, and to the western on just as strong resemblances in other respects. The fact that so little is known of the breeding ranges of the two forms is an added reason for conservative systematic treatment of non-breeding birds.

***Heteroscelus incanus* (Gmelin).** Wandering Tattler

An adult male, a single bird (no. 44655), was shot by Brooks at Carcross, the evening of May 25. It was presumably en route to its breeding grounds farther inland.

***Actitis macularia* (Linnaeus).** Spotted Sandpiper

Seen at Carcross, May 22. Abundant in the Atlin region. Breeding along the lake shore and along stream beds; inevitably encountered wherever conditions are favorable. During the second week in June unfinished nests and incomplete sets were found; by the third week in July young birds had appeared; by the middle of August the young were full grown and in the first fall plumage. The last spotted sandpiper was seen at Surprise Lake, September 15.

***Numenius hudsonicus* Latham.** Hudsonian Curlew

One was shot near Atlin by one of the residents of the town, about the middle of May, shortly before our arrival. I saw the mounted bird. This is of interest as an inland occurrence of an usually maritime species; I know of no other occurrence in British Columbia away from salt water.

***Oxyechus vociferus* (Linnaeus).** Killdeer

At Atlin, May 28, a pair of killdeers were found established in a marsh immediately behind the town. They were seen there several times, but apparently left without successfully nesting. On July 7 a single bird was seen on the shore of Lake Como, and on July 10 one was flushed from a marshy spot in dense woods near that lake. These occurrences constitute probably the northernmost records of this species so near the coast, though inland it has been found somewhat farther north, to Great Slave Lake.

***Charadrius semipalmatus* Bonaparte.** Semipalmated Plover

Present at Carcross, May 22, and at that time in pairs and evidently ready to nest. Fairly common in the Atlin region; that is, a pair or

two could be found wherever conditions were favorable, a gravelly or sandy shore being the main requisite. The birds were noisy and solicitous on the breeding grounds. The sitting bird left the nest at the first appearance of an intruder in the distance, and male and female together hovered about, calling overhead or fluttering painfully over the ground with wings and tail outspread and dragging.

A nest was found June 10, containing four eggs, heavily incubated. This was in a gravelly area of wide expanse where Pine Creek empties into Atlin Lake, a locality that held at least three pairs of the plovers. The nest was in hard gravel, a depression about one inch deep and with vertical, sharply defined walls, the hole partly filled with small chips of wood and a few coarse straws. The eggs were placed perpendicularly, points down.

On June 20 the first young were seen, just hatched. The last semi-palmated plover, a single bird, was seen at Como Lake, August 21. Two specimens were collected (nos. 44656-44657), both newly hatched young, one taken June 20, the other, July 21.

#### ***Aphriza virgata* (Gmelin). Surf-bird**

A single bird was shot by Brooks at Carcross, on the morning of May 27. It was taken at the same spot as the wandering tattler of two days before.

#### ***Dendragapus obscurus flemingi* Taverner. Fleming Grouse**

Nine specimens were collected by me (nos. 44658-44665, and one, unnumbered, presented to Allan Brooks). The series includes one small chick changing from natal down to juvenal plumage; one young male nearly through the post-juvenal molt; two old cocks, two years old or more; two males of the previous summer; two females in fully acquired first winter plumage; one adult female just through the annual molt. Brooks collected additional specimens, old and young, all of which I examined, and there are at hand, from previous expeditions in northern British Columbia, five adult females and three birds in juvenal plumage throughout. During the late fall following my departure from Atlin, Mr. A. B. Taylor, of that place, secured for me twelve additional specimens (nos. 46091-46102), six males and six females, some fully adult and some birds of the year. These constitute an invaluable series, as all are in freshly acquired fall plumage.

All this material affords an opportunity both for determining the characters of the subspecies *flemingi* and for following some of the complicated plumage changes that are undergone by grouse of this genus.

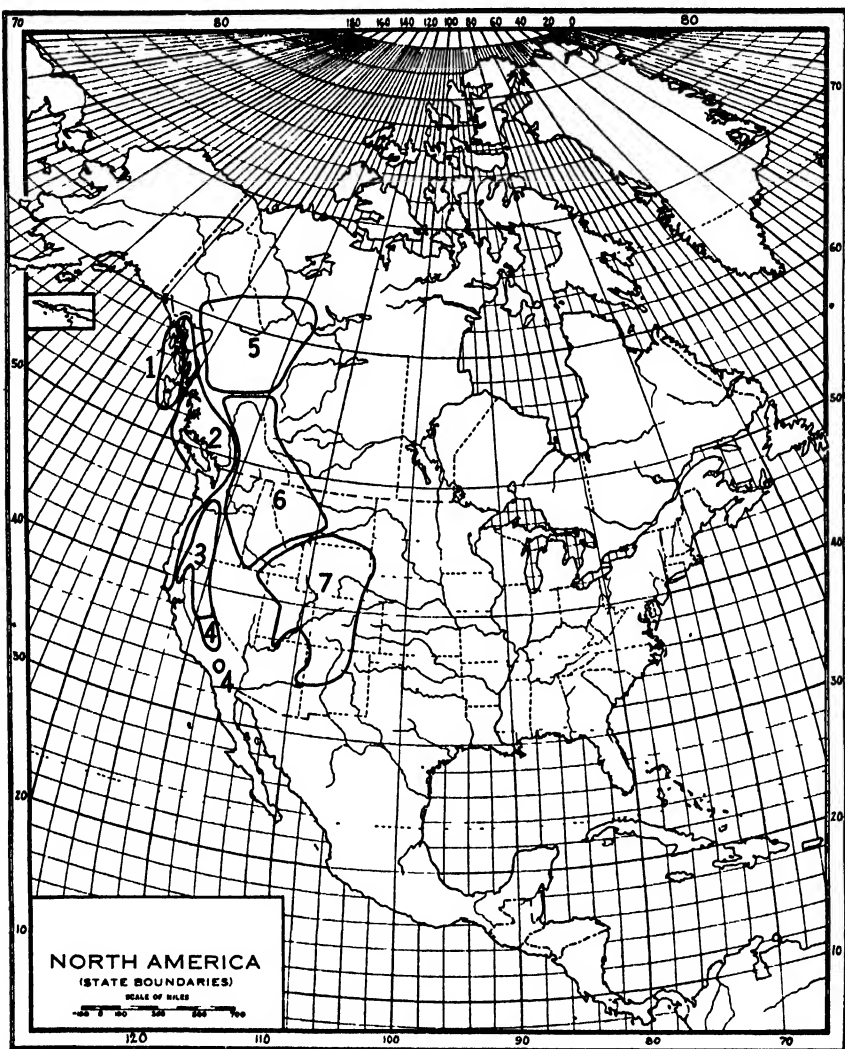


Fig. A. Map showing distribution of grouse of the genus *Dendragapus*: 1, *D. fuliginosus sitkensis*; 2, *D. f. fuliginosus*; 3, *D. f. sierrae*; 4, *D. f. howardi*; 5, *D. obscurus flemingi*; 6, *D. o. richardsonii*; 7, *D. o. obscurus*.

The type locality of *flemingi* is given by Taverner (1914, p. 386) as "near Teslin Lake." The country about Teslin Lake is mostly lowland, with not much mountainous territory suitable to this species.

I learned that the man who collected the type series of *flemingi* (a trapper, who sold specimens to the Canadian Geological Survey) had had his headquarters at Nisuttlin Bay, on the east side of the lake, and, from what I was told, in all probability his birds were shot on a low mountain that rises some four or five miles north of that point.

*Flemingi* is unquestionably closely related to *richardsonii* and much farther removed, genetically, from the coastal forms of *Dendragapus* whose ranges it approaches so nearly on the westward. In the descrip-

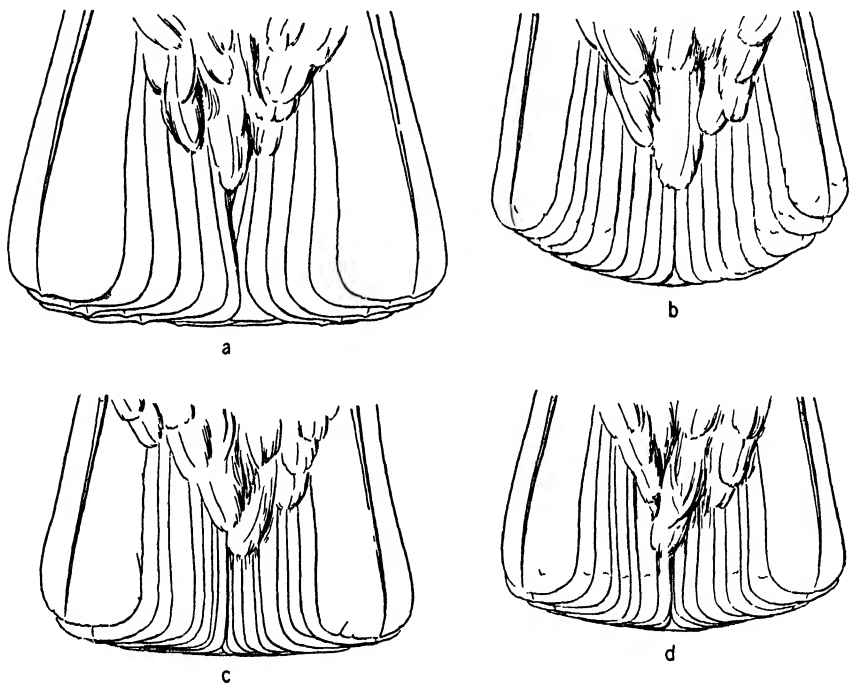


Fig. B. Tails of *Dendragapus obscurus flemingi*, showing variation due to sex and age; about  $\frac{1}{2}$  natural size. *a*, adult male, in second year or older (M. V. Z. no. 46091); *b*, immature male, during first year (M. V. Z. no. 46092); *c*, adult female (M. V. Z. no. 42001); *d*, immature female (M. V. Z. no. 46093).

tion of *flemingi*, Taverner (*loc. cit.*) properly makes most of his comparisons with *richardsonii*, as its closest relative, but he lays undue stress upon certain features that are of no systematic import. In the description of the tail he says: "Tail feathers not having the same chopped off appearance. Middle and several lateral feathers slightly to markedly double-rounded at end." This is a matter of age (see figs. B and C); the shape of the tail is the same in both subspecies.



The distinguishing feature between the two is color. The adult male of *richardsonii* is grayish in general appearance with some light brown mottling on back and sides. In *flemingi* the brown markings are much reduced and of a darker shade; in general appearance the fully adult male bird is almost black. In the adult female and in immatures (natal down and juvenal plumage of *richardsonii* not seen), corresponding differences exist. In most cases the distinctions between the two subspecies are evident upon the most cursory examination, and with the exception of one specimen they are uniformly maintained throughout the series at hand. The exception is an immature female of *flemingi* (no. 44665, head of Surprise Lake, Atlin region, September 14, 1924), which is much paler than others from the same general region, and hardly to be distinguished from a selected specimen of *richardsonii* from southern British Columbia. This bird may be taken to exemplify intergradation by individual variation between the two subspecies.

The sequence of plumage-changes with age in the grouse of the genus *Dendragapus* is sufficiently complicated to be difficult to follow, and extensive series of specimens are needed to trace the different stages. An understanding of the development of the individual bird is, however, absolutely necessary in order to avoid mistakes in making comparisons between the several forms included in this group.

Taking the subspecies *flemingi* as a basis, the following stages may be described as indicating the course of development followed in these grouse. Dates given apply to conditions in northern British Columbia.

Natal down: Sexes alike. There is no specimen of *flemingi* at hand entirely in the down, but comparing small young, still down-clothed on head and breast, with specimens of *sitkensis* and *fuliginosus* at the same stage, young *flemingi* is seen to be much less yellow, more gray, than are the young of those forms.

Juvenal: Again much more gray than in *sitkensis* and *fuliginosus*. Rectrices and remiges begin to appear a few days after hatching, and the young birds are able to fly long before the natal down is all lost. The head and neck are the last parts to be clothed in feathers, as shown in a specimen collected July 8. There is continuous replacement of plumage on the wings from the time the bird is hatched until it has finally completed the post-juvenal molt and is practically full grown. As shown by specimens of young *flemingi* and of other subspecies also, there are two complete sets of primaries, secondaries, tertials, and greater coverts, at least, acquired during the juvenal stage. The

newly hatched bird grows a set of small-sized wing feathers to accord with the tiny wing, and these are molted and replaced with others of the same juvenal type but of larger size. This can be demonstrated by measurement of corresponding feathers upon the wings of young birds of different ages.

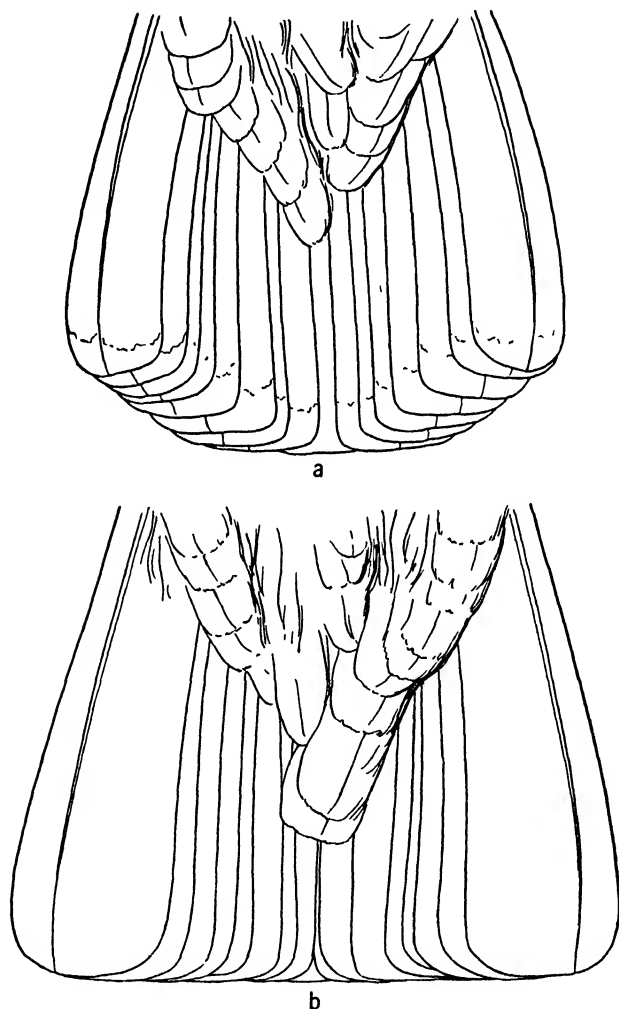


Fig. C. Tails of *Dendragapus obscurus richardsonii*, showing variation due to age;  $\frac{1}{2}$  natural size. a, immature male, during first year (M.V.Z. no. 42642); b, adult male, in second year or older (M.V.Z. no. 533).

First winter plumage (male): The sexes are unlike at this stage, nearly as much so as in the fully mature birds. The post-juvenal molt begins late in July or early in August, inaugurated by the shedding

of the juvenal rectrices (as pointed out by van Rossem, 1925, p. 417), and continues until nearly the middle of September. It may not continue over this entire period in the case of any one bird, but the time indicated is when the young, as a group, are undergoing this molt. The molt of the tail begins with the outermost feathers and progresses toward the middle. As in the post-natal molt, the head and neck are almost the last parts affected. The very last feathers to be changed appear to be the tertials. Juvenal tertials may be found on birds otherwise entirely in first winter plumage, as in two females at hand, collected September 14 and 15, respectively. The male in first winter plumage is in general like the fully adult except in tail character. The young male (until the end of the second summer) has the tail rounded, with the individual feathers relatively narrow and rounded. As a rule it has the tail more distinctly gray-tipped than is the case in adults. Minor color characters that appear in the first winter plumage, as compared with the fully adult, are: much more white spotting on upper breast, sides, and flanks; on the wings, the primaries, secondaries, tertials, and coverts are all more extensively mottled with rusty.

Adult plumage (male): The first post-nuptial molt begins about the middle of July of the second year and lasts until about the middle of September. The change in character of rectrices is the one conspicuous feature of the mature plumage. I cannot find that there is any renewal of rectrices (except sporadically, presumably as the result of accidental feather loss) until this molt regularly begins. This, I believe, is the only point in which I disagree with van Rossem (1926, pp. 417-422) in the conclusions drawn by him regarding molt in this genus. The fully adult tail, now acquired, is square ended, the feathers broad and truncate. Minor color differences are a clearer gray coloration below and less white spotting on breast and sides, while the mottling on dorsal surface of wings and on interscapulars is less in extent, and gray instead of brown.

In the female the differences between first winter and later plumages are not so apparent, but here, too, the greater breadth of the tail feathers is a feature of the mature bird.

The several recognized forms of *Dendragapus* are currently regarded as being all subspecies of one species, *Dendragapus obscurus*, but it seems to me that there are, rather, two species involved in this assemblage. Under the species *Dendragapus obscurus* I would place (from north to south) the subspecies *D. o. flemingi*, *D. o. richardsonii*, and *D. o. obscurus*. Under the species *Dendragapus fuliginosus* I

would place as subspecies, *D. f. fuliginosus*, *D. f. sitkensis*, *D. f. sierrae*, and *D. f. howardi*. The differences between the *obscurus* and *fuliginosus* aggregations are trenchant ones and I have seen no doubtful specimens, no "intergrades," from regions where the two come closest together. There are various statements in literature affirming the existence of intergradation between *obscurus* and *fuliginosus*, but these are all assertions of the most casual nature, with no detailed information accompanying them.

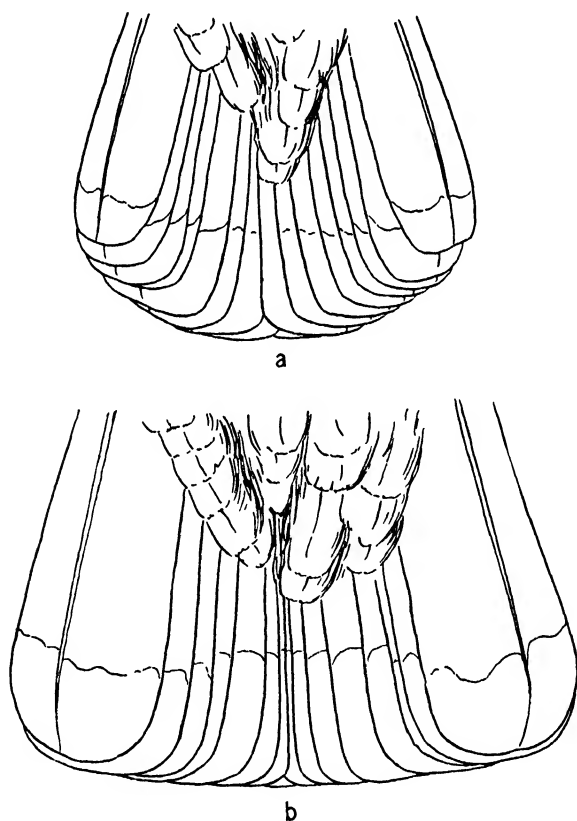


Fig. D. Tails of *Dendragapus obscurus obscurus*;  $\frac{1}{2}$  natural size. *a*, immature female, during first year (M.V.Z. no. 32051); *b*, adult male, in second year or older (M.V.Z. no. 45556).

In this connection it is pertinent to note conditions at Log Cabin, on the east slope of White Pass, about on the boundary between the ranges of *fuliginosus* and *flemingi*, where Brooks hoped to collect specimens of grouse that would have bearing on this problem. He, himself, found no *Dendragapus* there, and he was told by residents that none occurred in that stretch of country.

As between the two aggregations, *obscurus* and *fuliginosus*, besides color differences and besides the shape of the tail, so markedly contrasted in the closely adjacent northern subspecies, account must be taken of the call-notes of the male birds, which are so radically different as to indicate a wide divergence and one of long standing, a specific difference. The reverberant, wooden call of an old "hooter" (*Dendragapus fuliginosus*) is the same from Alaska to southern California, a sound that carries a half-mile or more, and a very different call from the subdued tooting of the Richardson grouse and its allies. Complementary to this, the relative development of a part of the hooting apparatus, the naked skin on the sides of the neck, is another difference between the two forms (see Brooks, 1912, p. 252; 1926, p. 283).

It looks as though in all the earlier studies of these grouse the presence of a terminal gray band on the tail alike of *obscurus* and of *fuliginosus* was allowed to outweigh all other features of resemblance or dissimilarity between the several forms. Aside from this, an adult male of *obscurus* is very closely similar to an adult male *richardsonii*. The tail of an adult male *obscurus* at hand, from Colorado, is nearly as square as in *richardsonii*, not rounded as in *fuliginosus*. The rectrices of *obscurus*, however, are not markedly truncate.

In years past *richardsonii* has sometimes been regarded as a species, distinct from the several other forms of "blue grouse," all regarded as subspecies of *D. obscurus*, but study of a map outlining the distribution of the races will show how illogical such division would be (see fig. A).

It is curious to what an extent certain of the characters of *richardsonii* parallel the distinguishing features of *Canachites franklinii*. This grouse (which is currently regarded as a species, distinct from other forms of *Canachites*) has developed the same square-tipped tail with broad, truncate feathers, and, besides this striking resemblance, the distribution of the Franklin grouse is almost the same as in the Richardson grouse; almost, but not exactly, for northward the range of *Canachites franklinii* extends well within the territory of *Dendragapus o. flemingi*. In the northern portion of its range, *D. o. flemingi* is accompanied by *Canachites canadensis osgoodi*.

In differentiating the several subspecies of "blue grouse" (both species), shape and markings of the tail are useful characters, but to ascribe proper weight to these variations an understanding is necessary of the development of the individual bird, of the stages gone through to reach maturity, as previously indicated in this paper. In both sexes

of all the forms of *Dendragapus* there is more or less variation with age in the shape of the tail feathers, in the length of the tail, and in the shape of the tail as a whole.

In the plumage as a whole there is marked seasonal variation, too, that must be taken into account. Birds in fresh fall plumage (both sexes and both the yearlings and fully mature) are of a clearer blue-gray, compared with late spring and summer specimens, in which this color has changed to a dingy brown.

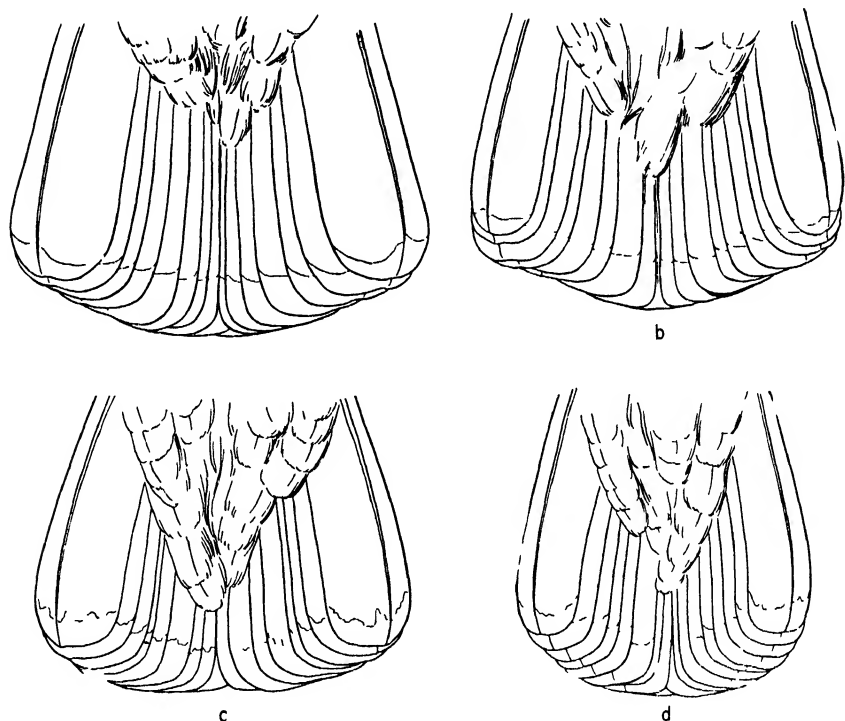


Fig. E. Tails of *Dendragapus fuliginosus sitchensis*, showing variation due to sex and age, about  $\frac{1}{2}$  natural size. a, adult male, in second year or older (M.V. Z. no. 133); b, immature male, during first year (M.V.Z. no. 136); c, adult female (M.V.Z. no. 134); d, immature female (M.V.Z. no. 135).

Relative roundness of tail, besides being a marked age character in certain forms, is also a feature in geographical variation. The subspecies *howardi* was described as having the tail longer and more graduated than *sierrae* (Dickey and van Rossem, 1923, p. 168), and the comment is made that "throughout the range of *Dendragapus obscurus* in California there is a gradual geographic variation which particularly affects the length and graduation of the tail." This same variation can be traced beyond California. From the northern limit

of the species *Dendragapus fuliginosus* in southeastern Alaska to its southern limit at Mt. Pinos, California, there is a steadily increasing degree of graduation in the tail. The same sort of geographical variation (that is, shape of tail) is seen to some extent in the *richardsonii* group. *Flemingi* and *richardsonii* are alike in possessing square-tipped tails, but the more southern form, *obscurus*, has the tail slightly rounded.

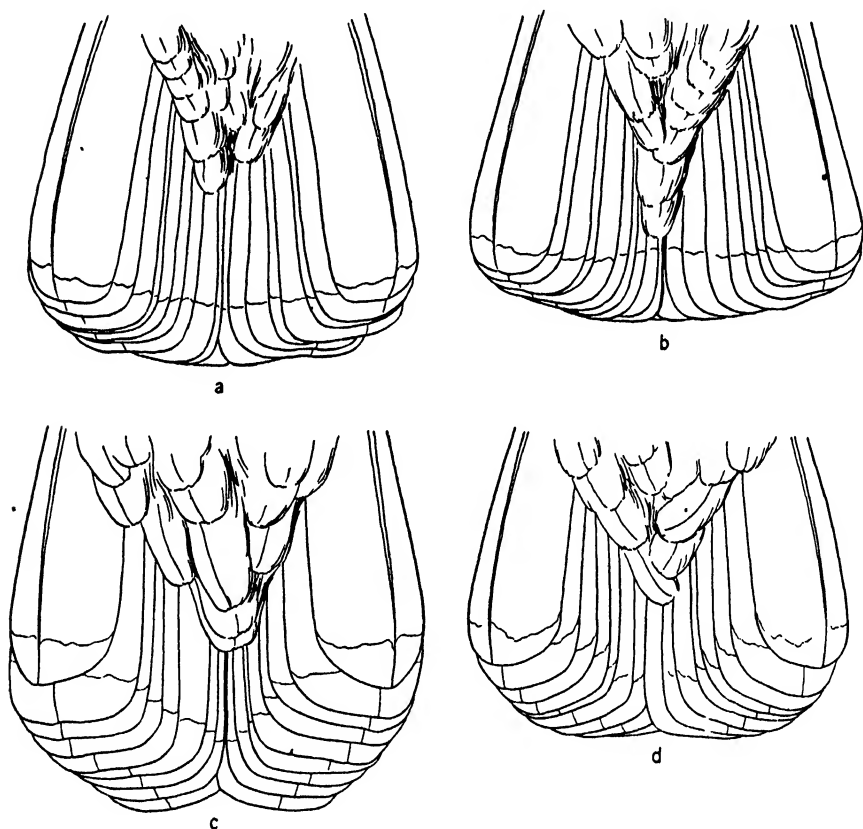


Fig. F. Tails of *Dendragapus fuliginosus sierrae* and *D. f. howardi*; about  $\frac{1}{2}$  natural size. a, *D. f. sierrae*, adult male (M.V.Z. no. 5082); b, *D. f. sierrae*, adult female (M.V.Z. no. 14069); c, *D. f. howardi*, adult male (coll. D. R. Dickey, no. K-240); d, *D. f. howardi*, adult female (coll. D. R. Dickey, no. J-881).

In the more southern subspecies of the *fuliginosus* group the gray terminal tail band is notably broader than in the northern races. In the southern *obscurus*, again, this feature is prominently developed, in contrast to conditions in the more northern *richardsonii* and *flemingi*, where it is all but absent.

In the course of this study I had occasion to examine five adult *Dendragapus* (in the D. R. Dickey collection) from the coastal side of White Pass, above Skagway, Alaska, and, most unexpectedly, these birds proved not to be of the subspecies *sitkensis*. They are exactly similar to specimens of *fuliginosus* from Vancouver Island. Prior to this I had seen but two specimens of *Dendragapus* from a mainland point in Alaska, a male and a female from Glacier Bay. The female was recognized as darker colored and less reddish than any island specimens of *sitkensis*, but it is in badly worn plumage, and this worn condition, it was assumed, might account in part for the difference.

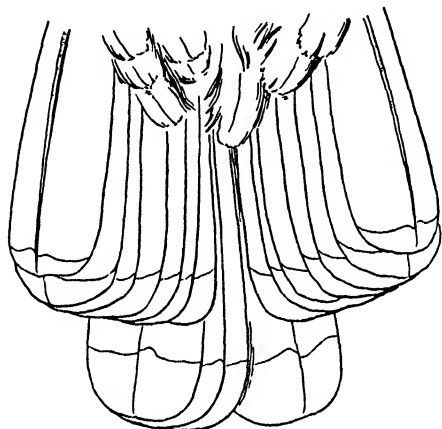


Fig. G. Tail of *Dendragapus fuliginosus fuliginosus*, showing variation due to age; immature male (M.V.Z. no. 15579);  $\frac{1}{2}$  natural size. Four central immature rectrices were lost by this bird in some way other than by the regular molt. The four longer rectrices that replaced them are of the adult type. The shorter lateral rectrices are of the immature type and have their full length. This bird, shot June 22, would not have molted for two months.

In the light of the additional specimens from Skagway, however, a revision of this view is necessary. It looks as though the subspecies *Dendragapus fuliginosus fuliginosus* must occur northward continuously along the mainland coast of British Columbia and southeastern Alaska, leaving *sitkensis* restricted to an island habitat.

In the Atlin region the "blue grouse" is resident and fairly common at high altitudes. It is a favorite game bird of the region, both from its large size and from the excellent quality of its flesh. Its habitat is about timber line, where there is open country interspersed with clumps of balsam firs. The dense thickets of these stunted trees, with their gnarled and spreading branches, afford shelter from enemies and from inclement weather, and in the foliage food also is furnished when other sources fail.



Small chicks were seen on July 8. By the first of September young birds were nearly finished with the post-juvenal molt, and about two-thirds the size of adults by measurement, though of only one-half the weight. The broods are cared for solely by the hen. The old cock is usually solitary during the summer, though males of the previous year sometimes form small coveys, together with non-breeding females. Such gatherings were encountered on several occasions. The hen with a brood is sometimes tame to the verge of stupidity; I found several that were, literally, as indifferent to approach as any barn-yard fowl. I have, however, seen an occasional covey of young birds that was extremely hard to approach. The broods often feed over open meadows, where they are exposed to attack by hawks and other enemies, and there must be a heavy mortality from such causes. That this is borne out by the small size of most of the broods encountered, and by the number of hens seen with no broods at all.

Following is a list of subspecies of the grouse of the genus *Dendragapus*, arranged according to their geographical position, from north to south.

1. *Dendragapus obscurus flemingi* Taverner. Fleming Dusky Grouse.
2. *Dendragapus obscurus richardsonii* (Douglas). Richardson Dusky Grouse.
3. *Dendragapus obscurus obscurus* (Say). Colorado Dusky Grouse.
4. *Dendragapus fuliginosus fuliginosus* (Ridgway). Oregon Sooty Grouse.
5. *Dendragapus fuliginosus sitkensis* Swarth. Sitka Sooty Grouse.
6. *Dendragapus fuliginosus sierrae* Chapman. Sierra Sooty Grouse.
7. *Dendragapus fuliginosus howardi* Dickey and van Rossem. Mount Pinos Sooty Grouse.

***Canachites canadensis osgoodi* Bishop. Alaska Spruce Grouse**

Ordinarily this is a common species in the region, but in 1924, for some reason that was not obvious, spruce grouse had declined in numbers to a point of actual scarcity. Single birds were flushed at long intervals, as were occasionally hens with their broods, consisting of one, two, or three chicks. No larger broods were seen. Early in September, traveling from Atlin to Lake Teslin and back, a week's trip, I saw all told only ten or twelve spruce grouse. This was in country that was throughout suitable to the species, and where during other years it had been found in abundance.

The spruce grouse is primarily a lowland species in the Atlin region. In the valleys it occupies the spruce woods almost entirely, being

rarely seen in the groves of poplar (the principal deciduous forest tree), and it follows the spruce up the mountain sides as far as that tree goes. We saw none in the balsam woods of slightly higher altitude, where the blue grouse (*Dendragapus*) is found.

Twelve specimens of spruce grouse were collected (nos. 44666–44677): two adult males, one adult female, one downy chick, near Atlin, June and July; one adult male, Spruce Mountain, August 8, nearly through the molt; one adult female and one immature male, Atlin, August 27, both finishing the molt; one male, Gladys Lake, September 9; one male and three females, Fat Creek, five miles west of Lake Teslin, September 13.

These birds were all taken within fifty or sixty miles of Lake Marsh, the type locality of *osgoodi*, and may fairly be assumed to be typical of that subspecies. Through the courtesy of Dr. L. B. Bishop I have been able to examine three near-topotypes of *osgoodi*, females from Lakes Marsh and Lebarge, but these birds, taken in July, are in such worn plumage as to be of little value for color comparisons. Most of the specimens from southern Yukon and northern British Columbia are appreciably different from birds from the northern limits of the habitat of *osgoodi*, as currently defined. Northern Alaskan birds exhibit the extreme of grayness seen in the species *Anachites canadensis*. One female taken in June at Atlin is as gray as any of the more northern birds, but the rest of the series are less overcast with grayish dorsally, less heavily marked with white on the breast, and are generally more richly colored. For the present it seems best to continue to use the name *osgoodi* for the race of spruce grouse occurring from northern Alaska south into northern British Columbia, but future collecting, especially of series from Alberta and Mackenzie, may show the desirability of a different arrangement.

### ***Bonasa umbellus umbelloides* (Douglas). Gray Ruffed Grouse**

An uncommon species in the Atlin region, in our experience. An occasional cock bird was flushed in poplar thickets, and two broods of young were seen during the summer. Aside from the chicks, not more than eight or ten birds, all told, were seen. Two specimens were collected (nos. 44678–44679), adult males, taken September 19 and 21, respectively.

**Lagopus lagopus albus** (Gmelin). Southern Willow Ptarmigan

Specimens of willow ptarmigan collected by myself in the Atlin region include three adult males and one adult female in summer plumage, two in natal down, two in juvenal plumage, twelve adult males and five adult females in "winter plumage, preliminary" or partly in that plumage, five immature males and two immature females, mostly in first "winter plumage, preliminary," a total of thirty-two skins (nos. 44680-44711). Additional specimens collected by Brooks near Atlin and near Log Cabin were also at my disposal.

In previous papers I have used the name *alexandrae* for the willow ptarmigan of British Columbia, but this additional mainland material, together with a large series of *alexandrae* from the Alexander Archipelago, southeastern Alaska (in the collection of George Willett), now available, demonstrates differences that exist between the two.

Riley (1911, p. 233) divided the willow ptarmigan of the North American mainland into two subspecies, *Lagopus lagopus ungavus* from the region east of Hudson Bay, and *L. l. albus* from the region to the westward. *Ungavus* he describes as having a heavier bill than *albus*. The range of *albus* is given as "from the west side of Hudson Bay, west through northern Alaska to eastern Siberia."

Clark (1910, p. 52), on the other hand, had previously said of the mainland birds (to which he gives the name *Lagopus lagopus albus*) that "all those from Labrador and central arctic America, with others from Point Barrow, Kotzebue Sound, Cape Lisbourne, Kowak River, Yukon River, and near St. Michaels, belong to a well-differentiated race, with the beak very large, high, and stout, the culmen strongly arched, and usually with a prominent ridge from the inferior corner of the maxilla to in front of the nostril. They are identical among themselves, it being impossible to tell from the examination of any one specimen whether it was taken in Alaska or in Labrador."

Thayer and Bangs (1914, p. 4) described *Lagopus lagopus koreni* from eastern Siberia, as differing from the willow ptarmigan of northern Alaska in its still heavier bill.

Differences which I had previously noted between British Columbia ptarmigan and those from northern Alaska were not to be reconciled by either Clark's or Riley's treatments of the races, and compelled further comparisons. Through the courtesy of Dr. Alexander Wetmore, Assistant Secretary of the Smithsonian Institution, I was enabled to borrow from the United States National Museum three specimens of

willow ptarmigan (*Lagopus lagopus albus*) from the west coast of Hudson Bay, and ten (*L. l. ungavus*) from Fort Chimo, Ungava. Comparison of these birds with the series in this museum convinced me of the existence of the following recognizable subspecies of the willow ptarmigan on the North American mainland: (1) *Lagopus lagopus ungavus* from the region east of Hudson Bay, as defined by Riley (*loc. cit.*); (2) *Lagopus lagopus albus* from the west shore of Hudson Bay westward to the coast ranges of northern British Columbia, and for an undetermined distance northward; (3) an undescribed subspecies from the Alaskan mainland and extending for an undetermined distance eastward in the extreme north.

To clear the ground for further discussion the Alaskan bird may now be described, as follows:

### ***Lagopus lagopus alascensis*, new subspecies**

#### **Alaska Willow Ptarmigan**

*Type*.—Male; no. 32125, Mus. Vert. Zool.; Kowak River Delta, Alaska; June 20, 1899; collected by J. Grinnell; original no. 4031.

*Distinguishing characters*.—Slightly larger than *albus*. A large-billed race; bill slightly smaller than in *ungavus*, much larger than in *albus* (see fig. H). In summer plumage, generally more reddish-colored than either *ungavus* or *albus*, a difference that is most conspicuous in females in the barred breeding plumage.

*Range*.—The Alaskan mainland except on the southeastern coast, northern Yukon Territory (specimens from vicinity of Forty-mile), and eastward for an undetermined distance.

Two males and one female ptarmigan at hand from the west side of Hudson Bay, one from Fort Churchill, July 24, and two from a point 75 miles north of York Factory, July 19, may be assumed to represent *Lagopus l. albus* (*Tetrao albus* Gmelin, 1788, p. 750, described from Hudson Bay). In bill structure they are like the British Columbia birds. In color the two males are like the British Columbia birds, but the Hudson Bay female is more reddish as compared with the gray-colored females of the latter series. Despite this difference in the females it seems best for the present to regard all as of the same subspecies, a small-billed southern race of the willow ptarmigan extending from Hudson Bay westward to the coast ranges of southeastern Alaska and northern British Columbia.

*Alexandrae* and *albus* are alike in possessing a small, slender bill, as contrasted with the heavy, more stubby bill of *alascensis*, and in color and markings they are closely similar in some plumages. Adult males in breeding plumage are essentially alike. The adult female of *albus* in breeding plumage (this and further allusions to *albus* refer to the British Columbia series) differs from the female *alascensis* in that stage, being much darker and less ruddy. The breeding female of *alexandrae* (one specimen from Porcher Island, British Columbia) is also a dark-colored bird but with a maximum of brown coloration in the plumage. The dark-colored female of *albus* has extensive blackish areas on the feathers, which are edged with dull brown or with grayish. In the dark-colored female of *alexandrae* there is an extension of rich brown markings on all parts of the bird.

Differences between *albus* and *alexandrae* are readily apparent in the "winter plumage, preliminary," that is, in the brown, late summer garb (the plumage stage inserted between breeding plumage or juvenal plumage, and the white winter plumage) in which both sexes and old and young become essentially alike—or would do so if this plumage were ever acquired in its entirety.

*Alexandrae* in this plumage is well represented in a series of specimens at hand collected by George Willett, mostly from Prince of Wales and Dall islands. In an adult male (Willett coll., Dall Id., September 3, 1919), head, neck, and body (except for a limited white area on the abdomen) are almost solidly dark brown, ranging from "brick red" to "Hessian brown" (Ridgway, 1912), with hardly a trace of vermiculation or mottling on the breast, and relatively little on the upper parts. In color tone and in markings on individual feathers there is extraordinarily close resemblance to winter specimens of the Scotch red grouse (*Lagopus scoticus*).

In *albus* in the same plumage, the browns are paler, there is much black or dusky barring and vermiculation, and dorsally the feathers are extensively black centered, and are gray tipped to such a degree as to affect the color tone of the whole upper surface. In *alascensis* the browns are still paler, and the black centers and gray tips of the dorsal feathers are almost or entirely lacking.

Conditions in these western races of willow ptarmigan parallel to some extent those found in the rock ptarmigan. In each species the northern Alaskan subspecies is an extremely ruddy-colored bird compared with the others, and in each the British Columbia subspecies seems to reach an extreme of grayness. In each species, too, the

Labrador birds are much more grayish than are those from Alaska. Thus the Labrador willow ptarmigan (*ungavus*) and the British Columbia bird (*albus*) are much alike as regards color but differ in size of bill. The Labrador bird and the northern Alaskan bird (*alascensis*) are both large-billed forms, but differ in coloration.

As regards the ranges of the several North American subspecies of *Lagopus lagopus*, it is not feasible at this time to indicate them with exactness. Series of birds from the Kowak River, Alaska, and from points on the Yukon as far upstream as Forty-mile, Yukon Territory,

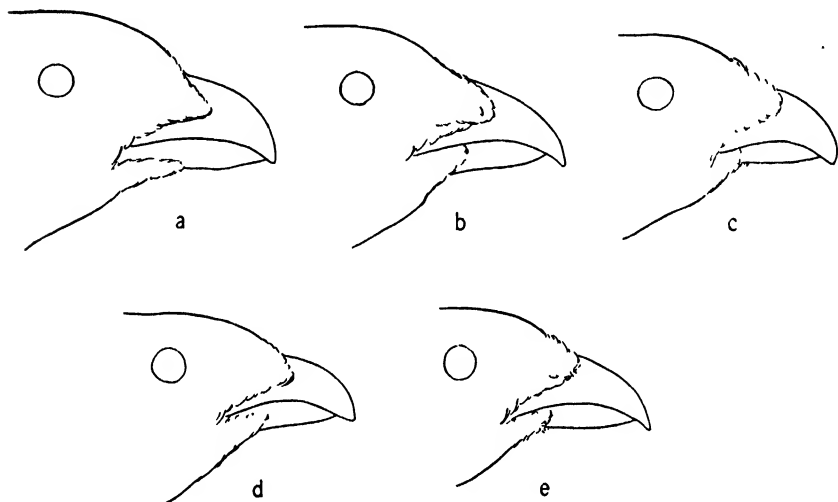


Fig. H. Bills of willow ptarmigan; adult males. *a*, *Lagopus lagopus ungavus*, coll. United States National Museum, no. 101037, Fort Chimo, Ungava; *b*, *L. l. alascensis*, M.V.Z. no. 32125, Kowak River delta, Alaska; *c*, *L. l. albus*, M.V.Z. no. 44681, Atlin, British Columbia; *d*, *L. l. albus*, United States Biological Survey, no. 167057, 75 miles north of York Factory, Hudson Bay; *e*, *L. l. alexandrae*, M.V.Z. no. 319, Baranof Island, Alaska.

belong to *alascensis*. A winter bird from a point 250 miles north of Edmonton, Alberta, is of the small-billed form, *albus*. Specimens collected by Brooks near Log Cabin, on the east side of White Pass, are *albus*.

*Lagopus l. alexandrae* is probably confined mostly to an island habitat, with perhaps a narrow strip of the adjacent mainland included, from Glacier Bay south to central British Columbia, at least as far as Campania Island. The series of *alexandrae* at hand shows some variation that may be correlated with distribution. Willett's specimens are all from Dall, Prince of Wales, and San Juan islands, in the southern portion of the habitat of the subspecies, and some of these, together

with a pair of breeding birds from Porcher Island (coll. Allan Brooks), still farther south, are distinctly darker colored than skins from the more northern Chichagof and Baranof islands and Glacier Bay. There are, however, some southern skins that are indistinguishable from northern ones.

On May 21 we traveled from Skagway to Carcross on the White Pass Railroad. Soon after passing the summit we began to see ptarmigan, and for an hour or more they were frequently in sight from the train, sometimes but a few yards from the track. The ground was still largely snow covered, though the snow was melting, and small ponds were partly free of ice. The male ptarmigan seen were with brown head and neck, the body plumage all white, and they were conspicuous objects. Courting was in progress and the cock birds, standing erect on projecting boulders or strutting with spread tail and lowered wings over some limited stretch of open ground, caught the eye from a long distance. A soaring *Buteo* flying alongside the train started birds in flight from several points.

On June 30 we found willow ptarmigan in fair abundance at the head of Cañon Creek (about 3000 feet altitude), near Atlin. They were in pairs, spaced at intervals through the low willow brush, and, from the broods seen, eggs must have hatched during several days immediately preceding. One nest was found, containing six eggs nearly ready to hatch. It was on a bare dry hillside; placed between two fallen saplings, just at the edge of some burnt spruce woods. Fire had passed through here years before, killing the timber, though most of the dead trees remained standing, and the ground beneath was barren of any vegetation. The nest itself was a shallow depression, scantily lined with a few bits of dry grass and weedstalks. The hen was sitting on the eggs and the cock bird was on guard nearby.

In this case, as in others, the devotion of the male willow ptarmigan was most apparent, and in striking contrast to the irresponsibility of the males of the other species of grouse of the region. Broods of young willow ptarmigan were invariably attended by both parent birds. It seemed evident that the large winter flocks of ptarmigan were formed by the junction of many families which had remained together, male, female, and young, since the eggs were hatched. It was very rarely that a solitary willow ptarmigan was flushed.

At the head of Otter Creek, July 26 to August 9, willow ptarmigan, though not abundant, were frequently encountered. Young birds were then about half grown, and in juvenal plumage throughout. The

willow ptarmigan frequented the floor of this valley and the lower slopes of the surrounding mountains. Their preferred habitat was a tangle of low willow and birch brush, with grassy open patches at intervals. None was seen on the higher ridges or the slopes higher than about 4000 feet; there this species was replaced by the rock and the white-tailed ptarmigans. •

On September 1, a trip was made to "Blue Cañon," a local name for a section of upper Spruce Creek some twelve to fifteen miles southeast of Atlin. Willow ptarmigan were then beginning to gather in large flocks. In the valley bottom relatively few birds were seen, though some were scattered all through this section, too; the center of abundance was on the lower slopes of the mountains, at from 3500 to 4000 feet. This was above the more extensive tangles of willow and trailing birch, and was a much more open sort of country. Thickets of dwarfed balsam, and some of willow and birch, were interspersed with open stretches, grass-covered or carpeted with *Empetrum* and other low-growing shrubs.

Willow ptarmigan, in flocks of from ten or twelve (single families, presumably) up to sixty or seventy, were within sight or hearing practically all of the time that we remained at that level. The larger flocks were, I was told, the first indication of much greater gatherings that were assembled during the winter months. On this date (September 1) specimens were taken of adults and young of both sexes.

Adult males taken in midsummer (June 30) in the breeding plumage retained a great deal of white on the belly, and these old white feathers apparently remain until replaced by white feathers at the end of August. Adult males taken September 1 are mostly white on the lower breast and abdomen. Adult females are mostly in the reddish "winter plumage, preliminary," to use the descriptive phrase originating with Dwight (1900), though always with many barred feathers of the breeding plumage persisting on breast and flanks, and some blackish feathers of the same plumage on the back. Over the whole belly the molt in every specimen examined was direct from the barred breeding plumage to white winter garb. There is an adult female of *alexandrae* at hand (Willett coll., Prince of Wales Island, Alaska, September 23, 1919) in the reddish post-breeding plumage, with but a few scattered barred feathers left. I have seen none from the interior that has assumed this plumage so nearly in its entirety. In the Atlin region it is evident that the white winter plumage begins to come in before the reddish "winter plumage, preliminary" is more than half acquired.



In young birds, too, the first "winter plumage, preliminary" is only partly acquired. Over the whole of the lower parts below the upper breast the molt is direct from the juvenal to the white winter plumage. On the head, neck, and dorsum, the "first winter, preliminary" is partly acquired, but white feathers appear on the chin and throat long before the juvenal plumage is lost on back and flanks. Young birds of *alexandrae* at hand (Willett coll.), taken in October, are in "first winter, preliminary," almost complete. There are but a few juvenal feathers left to distinguish young from old. In every case, though, young birds and adults may be distinguished by the differently shaped tertials, which linger longer than almost any other feathers of the brown-colored plumages.

On September 1, adults from the Atlin region had almost all acquired new flight feathers and rectrices. In the young, the juvenal rectrices are lost at a very early age, before the bird is half grown, being almost the first of that plumage to go. On September 1 nearly all young birds seen had completely acquired the black rectrices of the first winter plumage, slightly narrower than in adults but not otherwise different.

To summarize these details of plumage, they all go to show the incomplete nature of the "winter plumage, preliminary," inserted between the breeding plumage and the white winter plumage in adults, between the juvenal plumage and white winter plumage in young birds. Judging from material at hand it is less perfectly acquired at the northern limit of the range of the willow ptarmigan, and more perfectly acquired toward the southern limit, where longer summers give more time before the white winter plumage is essential. On the islands of southeastern Alaska, the habitat of *Lagopus l. alexandrae*, a region of relatively mild winters, the "winter plumage, preliminary" is acquired more nearly to perfection than perhaps anywhere else in the general range of the species. As a result of the perfect acquisition of this plumage in this particular dark-colored race, we see fall birds that closely resemble the Scotch red grouse (as described above), which bird, of course, is a southern species of *Lagopus* which does not acquire a white winter plumage at all.

In this account of the plumage variations of the several subspecies of the willow ptarmigan here under consideration I have used throughout the terminology employed by Dwight (1900, p. 147) in his exposition of the seasonal and other changes undergone by these birds. My own observations (made much easier through a previous reading of

## COMPARISON OF CHARACTERS IN DIFFERENT PLUMAGE STAGES OF THREE WESTERN NORTH AMERICAN SUBSPECIES OF LAGOPUS LAGOPUS

|   |   |  |   |
|---|---|--|---|
|   | <i>alascensis</i><br>Northern Alaska<br>Large-billed    | <i>albus</i><br>Northern British Columbia<br>Small-billed  | <i>alexandrine</i><br>Southeastern Alaska<br>Small-billed               |
| Adult male, spring (May and June).          | Paler; more ruddy dorsally                              | Generally darker colored   | Generally darker colored.   |
| Adult male, winter, preliminary.            | More ruddy dorsally; lighter brown on throat and chest. | More gray dorsally; lighter brown on throat and chest.   | Darker, more uniformly brown dorsally. Dark vinous on throat and chest. |
| Adult female, spring                        | Dark markings restricted; bright hazel.                 | Dark colored; browns duller and black areas larger; feather edgings dorsally gray rather than brown. | Brown areas extensive and richly colored; no gray dorsally.             |
| Adult female, winter, preliminary.          | Paler colored; bright ruddy                             | Darker; much gray on dorsum; chestnut areas darker.  | Much darker; no gray on dorsum; more uniformly brown (vinous).          |
| Male and female, first winter, preliminary. | Paler brown   | Paler brown; much gray on dorsum.  | Darker; almost uniformly brown (vinous) above.                          |
| Male and female, juvenal                    | Paler; more ruddy                                       | Less ruddy; more grayish   | Dark brown.   |

MEASUREMENTS IN MILLIMETERS (AVERAGE, MINIMUM AND MAXIMUM) OF THREE NORTH AMERICAN SUBSPECIES OF LAGOPUS LAGOPUS

|  |   |                      |                      |                  |                  |                  |
|--|---|----------------------|----------------------|------------------|------------------|------------------|
|  | Wing                                      | Tail                 | Culmen               | Depth of bill    | Width of bill    |                  |
| Lagopus l. ungavus, 5 adult males.     | Fort Chimo, Ungava.<br>July 14, 1884      | 194.4 (191.0-198.0*) | 120.8 (119.0-124.0*) | 20.0 (19.0-20.5) | 14.2 (13.0-14.8) | 13.3 (13.0-13.5) |
| Lagopus l. alascensis, 10 adult males. | Northern Alaska.                          | 199.4 (192.0-207.0)  | 124.3 (115.0-133.0)  | 17.1 (16.5-17.5) | 11.9 (11.2-12.5) | 12.4 (11.0-13.5) |
| Lagopus l. albus, 10 adult males.      | Atlin, British Columbia.<br>Sept. 1, 1924 | 188.3 (182.0-193.0)  | 122.3 (118.0-129.0)  | 15.6 (15.0-17.5) | 10.3 (10.0-11.0) | 11.4 (11.0-12.0) |

\* Very worn plumage.

Dwight's paper) accord with his statements, I believe, in every particular. Details here given are amplified in the belief that such studies from all parts of the range of the willow ptarmigan are necessary to a thorough understanding of geographical variation in this species.

LIST OF THE NORTH AMERICAN SUBSPECIES OF THE WILLOW  
PTARMIGAN (*LAGOPUS LAGOPUS*)

1. *Lagopus lagopus alleni* Stejneger. Allen Willow Ptarmigan.
2. *Lagopus lagopus ungavus* Riley. Ungava Willow Ptarmigan.
3. *Lagopus lagopus albus* (Gmelin). Southern Willow Ptarmigan.
4. *Lagopus lagopus alascensis* Swarth. Alaska Willow Ptarmigan.
5. *Lagopus lagopus alexandrae* Grinnell. Alexander Willow Ptarmigan.

***Lagopus rupestris rupestris*** (Gmelin). Gray Rock Ptarmigan

Thirteen specimens of rock ptarmigan (nos. 44712-44724) were collected by myself in the Atlin region, including seven adult males, two adult females, and four young birds. Brooks' Atlin series comprised about as many, similarly apportioned, and he later (September 11) collected at White Pass summit four additional specimens, two adult females and male and female immature.

• The ptarmigans form a group of birds that offers many difficulties to the systematist. The rapid and continuous changes of plumage undergone by any one bird during the summer months, together with a rather wide range of individual variation among specimens from any given locality, are puzzling features in themselves, still further complicated by other differences due to sex and age. Then, ptarmigan, and the rock ptarmigan in particular, are not well represented in collections, inhabiting, as they do, relatively remote and inaccessible regions. So, more often than not, when specimens are brought together from different sections they prove to be not comparable, and deductions then can only be made by inference.

In a previous publication (Swarth, 1924, p. 333) I have commented upon the appearance of a female rock ptarmigan from Nine-mile Mountain, near Hazelton, British Columbia, a bird that differed appreciably from the few Alaskan specimens available to me at that time. The series we collected near Atlin, evidently in the same category as the Nine-mile Mountain bird, seemed again so different from Alaskan specimens as to justify more extensive comparisons.

Through the courtesy of several museums and private collectors (to whom acknowledgment is made elsewhere in this paper) a series of 168 rock ptarmigan in summer plumage was brought together, representing many parts of the mainland of North America and some Arctic islands also. A few of these localities are represented by extensive series of summer birds, and some such points fortunately prove to be rightly placed to illustrate certain important features of geographical variation in the northwest. This study has not included the ptarmigans of the Aleutian Islands, Greenland, Newfoundland, and Anticosti.

In the portion of North America indicated, excluding the islands mentioned, the rock ptarmigan has differentiated into three easily recognizable branches. First, there is a gray-colored bird that extends from Labrador westward to the coast ranges of northern British Columbia. In the east it apparently extends northward into the Arctic regions; it also occurs on islands north of Mackenzie, but elsewhere in the west it is restricted to the southern part of the region covered by the species *Lagopus rupestris*. Second, there is a ruddy-colored form that occupies almost the entire mainland of Alaska and extends eastward along the Arctic coast about to the one hundredth meridian. Third, there is a dark colored form with a rather limited range in the coastal region of southeastern Alaska (see fig. I).

The first-mentioned race, the gray-colored bird, may probably be assumed to represent *Lagopus rupestris rupestris* (Gmelin), described from "Hudson Bay." It was the gray coloration of British Columbian birds, as compared with the ruddy Alaskan specimens, that first attracted my attention, and it seems evident that this gray race extends practically across the continent. There are two males and one female at hand from McLellan Strait, Labrador, and one female from the mouth of the Nastapoka River (east coast of Hudson Bay), Ungava. The two male birds can be matched exactly in the series of Atlin specimens. The female from McLellan Strait is even more gray than any of the British Columbia birds; the one from the Nastapoka River is indistinguishable from Atlin skins.

A half-grown juvenal from Ponds Inlet, Baffin Land, is a trifle more gray than comparable Atlin specimens, but very slightly so. The variation is no more than occurs within series from any one place. The locality of capture of this specimen might be considered as within the range of *Lagopus r. reinhardi* (see A. O. U. Committee, 1910, p. 141), but in appearance it certainly agrees with *rupestris*, as repre-

sented from other regions. There are few specimens available from intermediate points between the extremes of Labrador and British Columbia, but two females from Clinton-Golden Lake and Cap Mountain, Mackenzie, respectively, are unmistakably of the gray *rupestris* mode of coloration. Specimens from the Arctic islands north of Mackenzie are also to be referred to *rupestris*.

In my published comments upon the female rock ptarmigan from Nine-mile Mountain, British Columbia (Swarth, 1924, p. 333, fig. A), I described in detail the striking white tail markings seen in some birds from that region. This proves not to be a character of any systematic value. At the time we were shooting rock ptarmigan in the Atlin region they were molting their tail feathers, and many birds were flushed which, if they possessed this character, would not have shown it in their then condition. Several were shot with tail fully grown and with rectrices black throughout (save for the usual restricted white markings at base and tip), and several that exhibited white markings of irregular extent on some of the tail feathers. I found some molted rectrices where they had been dropped on the hillsides that were marked as in the Nine-mile Mountain bird. Among all the specimens assembled in the present study, just one bird, an adult female of *dixonii* from the White Pass, Alaska (D. R. Dickey coll., no. 13462), has this feature developed as in the specimen I figured. Judging from the material at hand, it would seem that this character occurs irregularly in the female bird in the extreme southwestern part of the range of the rock ptarmigan; irregularly in that it may or may not exist in individuals from any one place, in that it may occur on some tail feathers and not on others, and in that it may cover a greater or lesser area on corresponding feathers on different birds. Curiously, there is an adult female at hand, taken near Bennett, on the east side of the White Pass, September 11, 1924 (coll. of Allan Brooks), mostly in the white, winter plumage, in which the central (usually white) tail feathers are basally black, a condition I do not find in any other specimen.

The small size of bill in the Nine-mile Mountain bird was another feature that was commented upon in my previous paper. The larger series now available shows that while in the more southern birds the bill is frequently smaller than in any of the northern specimens, it is not a character to be relied upon. It can be described as a tendency of the southern birds.

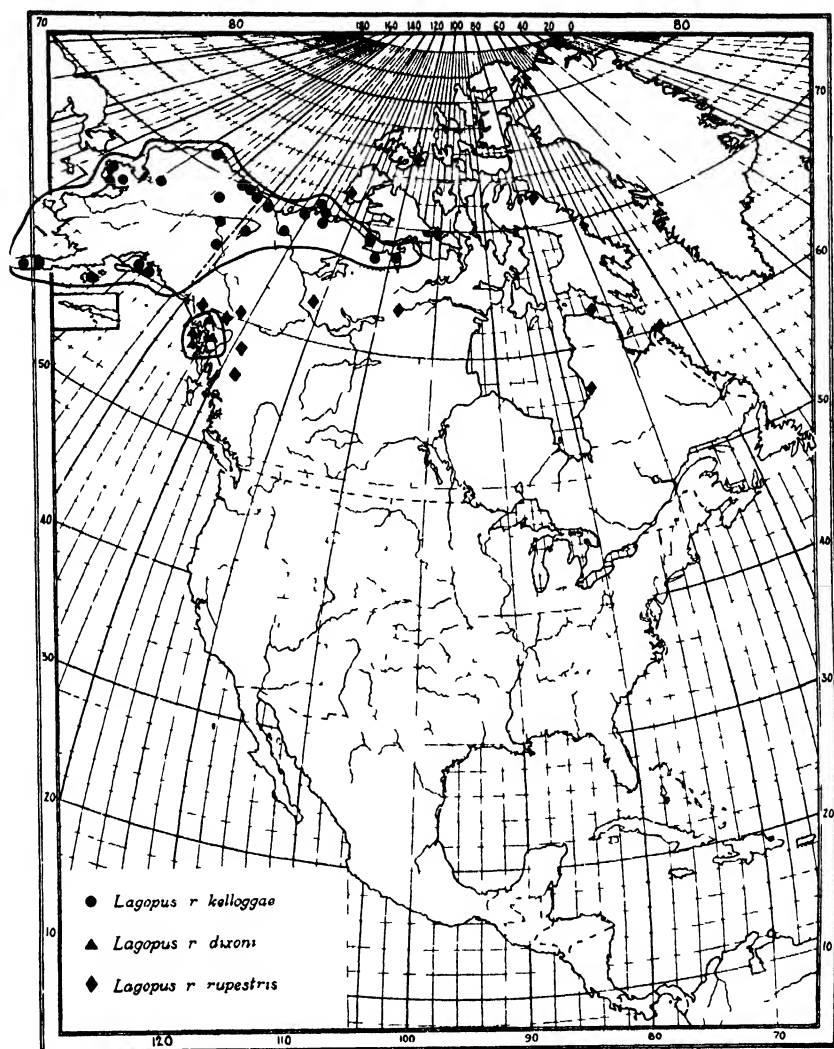


Fig. I. Map showing distribution of certain subspecies of rock ptarmigan (*Lagopus rupestris*). The approximate habitats of *L. r. kelloggae* and *L. r. dixonii* are outlined. Symbols indicate localities from which specimens were examined.

Next to be considered is the Alaska race. The notable feature of this bird is its bright ruddy tone of coloration, a character that is evident in both sexes and in all stages of the summer plumages. As compared with *rupestris*, the general tone of color throughout is brighter and more reddish, and there is notable restriction of the dark areas on individual feathers.

The extreme manifestation of this race is reached on the northwestern and northern coast of Alaska, it occupies practically the whole of the Alaskan mainland, and it extends eastward of Alaska along the Arctic coast for some distance. In the latter region the duller color of specimens from Baillie Island, Coronation Gulf, and Bathurst Inlet, is to be interpreted, to my mind, as indicative of intergradation with *rupestris*.

Southeastward there is intergradation again with *rupestris* as occurring in British Columbia, about at the Alaska-Yukon boundary line. A series of seventeen skins from the vicinity of Eagle (U. S. Biol. Surv. coll.), in the upper Yukon region, demonstrates such intergradation satisfactorily. Certain selected skins from this series and from the British Columbia aggregation are hardly to be distinguished, and none of the Eagle specimens shows the extreme of ruddiness that is seen in Alaskan birds from more northern points. The Eagle series as a whole, however, certainly belongs with the northern Alaska subspecies rather than with *rupestris*. On the southern coast there is apparent intergradation with *dixonii*, as shown by skins from Kodiak Island, Seward, and Prince William Sound.

The matter of a name for the Alaskan bird requires careful consideration. The race assuredly is distinct from *rupestris* of the Hudson Bay region, and as such is deserving of nomenclatural recognition. To have been able to fix a type locality somewhere in northern Alaska would have been desirable, for it is there that this form is developed in its extreme manifestation, but as it happens, the boundaries of the subspecies, as indicated by the specimens at hand, include a region from which a form of rock ptarmigan has already been named. I refer to *Lagopus rupestris kelloggae* Grinnell (1910, p. 383), type locality, Montague Island, Prince William Sound. It is true that in describing that subspecies Grinnell made detailed comparison with the same series of birds from Eagle to which I have already referred, and which I consider as belonging to the same race; and he based his belief in the distinctness of *kelloggae* partly upon the differences he could discern between birds from Prince William Sound and those from Eagle.

My own conviction of the desirability of including both series under the same name, rests upon the facts that birds from neither place are representative of the extreme manifestation of the Alaskan race; and that the differences between them are due to one series (from Eagle) illustrating intergradation toward *rupestris*, the other (from Prince William Sound) illustrating to some slight degree intergradation toward *dixonii*.

The type specimen of *kelloggii* (Mus. Vert. Zool., no. 1169, adult male, Montague Island, Prince William Sound, July 7, 1908) can be matched almost exactly by a selected specimen from Demarcation Point, Arctic coast of Alaska (Mus. Comp. Zool., no. 68933, adult male, July 10, 1914). Of the several Prince William Sound specimens, as with one adult male from the nearby mainland point of Seward, it seems to me that in whatsoever features they differ slightly from the mode of birds from northern Alaska, they show some approach toward *dixonii*.

For all these reasons I am regarding the name *kelloggii* as having been applied to a variant of the Alaskan mainland subspecies, and, with regard to the true features of this same subspecies, properly applicable to the whole aggregation.

There are fewer specimens of *dixonii* available than of either of the other subspecies here under consideration, but nevertheless this relatively scanty material suffices to show that it is a well marked form, and to indicate the range of the subspecies with fair accuracy.

*Dixonii* is a dark, slaty-colored race, with, in the male, the rufescent markings greatly reduced or altogether wanting. There are specimens at hand from Baranof and Chichagof islands, and from Port Snettisham and White Pass on the adjacent mainland. There is as yet no proof of the extension of the range of this form south of Christian Sound or north of White Pass. However, I have seen no rock ptarmigan from Yakutat Bay or from any other point on the long stretch of coast line between Lynn Canal and Prince William Sound, and *dixonii* may be found to extend for some distance in that direction.

The one specimen from Port Snettisham is a young female (Mus. Vert. Zool., no. 9796, August 29, 1909). Exactly comparable plumages are at hand from Atlin, from near Bennett, and from northern Alaska. From the Atlin birds it is widely different. The Atlin specimens are predominantly gray, the Port Snettisham specimen dark and rufescent. Two young birds from Bennett (coll. of Allan Brooks), though intermediate toward *dixonii*, are still much nearer to *rupestris* of the Atlin



region. The Port Snettisham bird differs but slightly from skins from Seward Peninsula and rather more so from young birds from the Arctic coast of Alaska. It is somewhat darker colored. It can be matched very closely by a young bird from Kodiak Island.

A pair of adults from Mount Dewey, on the Alaska side of the White Pass, are of especial interest. These are from the D. R. Dickey collection: no. 13462, female, July 26, 1923; 13463, male, August 7, 1923. The male bird is exactly like others from Baranof and Chichagof islands. The female is distinguished from other rock ptarmigan by dark tone and extremely rufescent coloration. It differs far more from Atlin females, and indeed from a female from Bennett, on the opposite side of White Pass, than from those from northern Alaska. Whether or not this specimen represents the mode of female *dixonii*, in its typical form, on Baranof and Chichagof islands remains to be seen. So far as I know there are no such specimens extant in any collection at this time.

The present study takes into account certain phases of geographical variation in the North American rock ptarmigan, and suffices to make clear some certain points, but there still remains far more work to be done before any satisfactory understanding can be reached of the manner of variation over the whole of the range of this species, or several species, as the case may be.

It may be pointed out that I have not touched upon the relations of the New World *Lagopus rupestris* and the Old World *Lagopus mutus*, which are admittedly close; the two forms may well be conspecific, as has been claimed (see Hartert, 1921, p. 1871). It is conceivable that the ptarmigan of northeastern Siberia is the same as the Alaskan subspecies here designated *Lagopus rupestris kelloggae*. The latter certainly attains its extreme of differentiation from *rupestris* on the Alaskan coast most nearly approaching Siberia.

I have not attempted to take into consideration such variation as occurs among the several forms described from the Aleutian Islands. There, too, a comprehensive study should help toward an understanding of the relationships of Old World and New World forms. The few specimens that I have examined from the Alaska peninsula exhibit, it seems to me, intergradation from *kelloggae* toward *nelsoni*, of the easternmost Aleutian Islands, but there is not at hand material to demonstrate this satisfactorily.

## SUMMER SPECIMENS EXAMINED

1. *Lagopus rupestris rupestris* (Gmelin). Gray Rock Ptarmigan.

Labrador: East end of McLellan Strait, 3.

Ungava: Mouth of Nastapoka River, 1.

Franklin: Hudson Strait, 2; Ponds Inlet, Baffin Land, 1; Griffith Point, Melville Id., 2; Cape Kellett, Banks Id., 2; Taylor Id., Victoria Land, 2.

Mackenzie: Clinton-Golden Lake, 1; Cap Mountain, 1.

British Columbia: Mountains near head of Chapatan River (headwaters of Stikine River), 3; near Atlin, 16; White Pass, 4; Nine-mile Mountain (near Hazelton), 3.

Total, 41.

2. *Lagopus rupestris kelloggae* Grinnell. Alaska Rock Ptarmigan.

Alaska: Collinson Point, 9; Demarcation Point, 4; Griffin Point, 5; Camden Bay, 1; Point Barrow, 1; Jade Mountains, 1; Gens de Large Mountains, 1; Iiula-hula River, 1; Okpela River, 1; Humphrey Point, 1; Nome, 1; Wales, 5; Teller, 2; Kruzgamepa River, Seward Peninsula, 24; Pilgrim River, Seward Peninsula, 4; Kings Cove, Alaska Peninsula, 2; Thin Point, Alaska Peninsula, 5; Kodiak Island, 1; Seward, 1; Montague Island, 1; Hinehinbrook Island, 2; Hawkins Island, 2; Fort Yukon, 1; mountains near Eagle, 17.

Mackenzie: Arctic coast east of Fort Anderson, 1; Fort Anderson, 1; Baillie Island, 3; Coronation Gulf, 8; Cape Bathurst, 1; Franklin Bay, 2; Kanyah Island, Bathurst Inlet, 2; Cockburn Point, 2; Bernard Harbor, Dolphin and Union Strait, 1.

Yukon Territory: Kay Point, Arctic Coast, 3.

Total, 117.

3. *Lagopus rupestris dixonii* Grinnell. Dixon Rock Ptarmigan.

Alaska: Port Frederick, Chichagof Island, 2; mountains near Sitka, 4; Port Snettisham, 1; White Pass, 2. Total, 9.

Our field experiences with the rock ptarmigan were productive of some facts of interest. One feature of the species (one that has been commented upon by others) was its irregular and local distribution. A male, a single bird, was shot by Brooks near the summit of Monarch Mountain, June 9. This was the only one that was seen by us on that mountain during the summer, though we ascended it many times.

On one of the ridges of Spruce Mountain, during the last week in July and the first two weeks in August, rock ptarmigan were found regularly and in fair abundance, every time we climbed that particular ridge. On an adjoining ridge, of similar aspect, none was seen, and certain other nearby mountains were also explored to no avail.

We visited rock ptarmigan territory too late to find nests, but from the actions of the birds as we saw them it would seem that the male of this species is not a devoted and constantly attendant mate to the hen, as is notably the case in the willow ptarmigan. The male rock ptarmigans were gathered, two, three, or four together, while the females bore the care of the young alone. Occasionally a female (presumably a non-breeding bird) was seen with several males. On August 8 I did flush a flock consisting of at least one brood of large young ones, and several adult males. This I took to be the beginning of a general flocking together, as might be looked for at the end of the summer.

The adult male taken on June 9 is still largely in winter plumage, especially below. There are barred feathers on the throat and upper breast, and the back is mostly clothed in summer plumage. Adult males taken during the last week of July and early in August are in summer plumage in as nearly perfect condition as it can probably ever be found, though in all the rectrices are being renewed. In the perfection of this plumage even the abdomen is partly or even entirely clothed in dark-colored feathers, but usually a large white area persists on the lower parts of summer birds. In some specimens old white body feathers are being replaced by new white ones, showing that there is not always an intervening dark summer plumage on parts of the body that are dark on some birds.

The adult male rock ptarmigan does not seem to go through the stage termed by Dwight (1900, p. 162) "second, or adult, winter plumage (preliminary)," that is so well defined in the willow ptarmigan. I am aware that the contrary has been argued (see, for instance, the account of *Lagopus ridgwayi* by Stejneger [1885, p. 195]), but whatever may be the facts as regards other forms of the rock ptarmigan, in British Columbia the male bird of this species does not exhibit two distinct plumages during the summer months. The female does, and the fact that we collected male birds during the period when the females (as well as both sexes of the willow ptarmigan) were molting from one plumage stage to the other, enabled me to make satisfactory comparisons of the different plumages. The first appearance of the brown and black barred feathers upon the head, neck, and upper breast in the male rock ptarmigan (early in June in northern British Columbia) is followed so uninterruptedly by the spread of more finely mottled feathers over the rest of the body, that these can hardly be considered as two distinct plumages. Furthermore, the first

acquired barred feathers of the neck and upper breast persist until replaced by white ones in the fall. Late in July and early in August the rectrices and remiges are renewed, accompanied usually by the appearance of the first white winter feathers upon the abdomen and flanks. The two white central tail feathers persist, in some cases at least, until the end of the summer, though they are hidden by long upper tail coverts. Whether or not these late retained feathers are at once replaced with other white ones I do not know.

The above remarks all pertain to the adult male. The adult female undergoes a more or less extensive molt, beginning late in July, following the barred breeding plumage and marking a well-defined plumage stage. She then acquires, above and below, finely mottled feathers like those of the male, but this plumage is never (or at any rate very rarely) acquired in its entirety before the white winter feathers appear. Young birds of both sexes begin a replacement of juvenal plumage with finely mottled feathers as in the adult, but here, too, the white winter feathers appear before the first change is accomplished. So quickly do the several molts follow one another during the summer months, that it is not uncommon to find female birds in August with remaining patches of white feathers from the previous winter, the greater part of the body clothed in the barred breeding plumage, some extensive areas of mottled feathers of the "winter plumage, preliminary," and some areas of new white feathers.

### ***Lagopus leucurus leucurus* (Swainson). White-tailed Ptarmigan**

Occurs, apparently not abundantly, at high altitudes. The predilection of this species for exposed, rocky ridges is reflected in the local name "rock ptarmigan." The few people we met who recognized the existence locally of three species of ptarmigan called the true rock ptarmigan by the name of "croaker."

I encountered the white-tailed ptarmigan on but one occasion, on September 1, when a flock of from fifteen to twenty birds was flushed on a rocky slope between the head waters of Spruce and McKee creeks, at about 5000 feet altitude. Three specimens were collected (nos 44725-44727), an adult female and a young male and female. In all three the lower breast and belly are clothed in new white winter plumage, the molt on those parts being direct from the barred breeding plumage in the case of the old bird, from the juvenal plumage in the young. Elsewhere these birds are entirely in the soft gray colors of the "winter plumage, preliminary."

**Circus hudsonius** (Linnaeus). Marsh Hawk

Found nowhere about Atlin during the breeding season. The first south-bound migrant appeared August 26; then, September 9 to 15, between Atlin and Lake Teslin, marsh hawks were seen in numbers flying southward. Last seen, near Atlin, September 21.

**Accipiter velox** (Wilson). Sharp-shinned Hawk

Seen at Skagway, May 21. Undoubtedly nests in the Atlin region, for occasional individuals were seen throughout the summer. Not common at any time, not even after the southward migration had begun. Last seen on August 29. One specimen collected, an immature male, August 18 (no. 44728).

**Astur atricapillus atricapillus** (Wilson). Eastern Goshawk

Undoubtedly nests in the Atlin region, probably in the lowlands, for individuals were seen at fairly frequent intervals throughout the summer. In August there was a noticeable increase in numbers, mostly of young birds, flying southward. Several immatures were shot but not preserved, and all were of the pale coloration that appears to be characteristic of the subspecies *atricapillus*. One specimen was skinned (no. 44729), a male in adult plumage, almost fully acquired, taken September 5. This bird is of interest in view of the argument advanced by Taverner (1916, p. 360; 1918, p. 216) that the goshawk molts from the streaked juvenal plumage into a coarsely barred stage (the subspecies *striatulus*) and later into the more finely barred plumage that is considered to be typical of the subspecies *atricapillus*.

The bird in question had just molted from the juvenal plumage. Very few juvenal feathers remain, but careful investigation before the bird was skinned showed enough old streaked feathers on various parts to demonstrate that this was the first assumption of adult plumage. This bird is pale colored and finely barred, as in *atricapillus*. Some of the breast feathers have rather broad mesial streaks but it is otherwise just like other specimens of *atricapillus* at hand, and very different from coastal examples of *striatulus*.

The status of the two forms *atricapillus* and *striatulus* cannot be regarded as settled, but the evidence at hand points to the existence of two such subspecies. Characteristic color differences occur in both

adults and young, and these differences are fairly well correlated with certain regions. The specimen just described (as well as another similar bird collected by Brooks) shows that differences of coarse or fine markings cannot be explained as different stages reached by the same individual.

The last goshawk was seen by me near Atlin, September 19, but it seems likely that the species remains to a later date.

***Buteo borealis harlani* (Audubon). Harlan Hawk**

I collected in the Atlin region six specimens (nos. 44730-44735) of a dark-colored *Buteo* that was of fairly common occurrence there. The series consists of one adult female, three young males, and two young females. Two of the young birds are just out of the nest, partly feathered and not able to fly any distance, the other three are full grown. In addition, Brooks collected an adult female and one young bird. There are at hand also two specimens loaned by the Provincial Museum, Victoria. Both are from the Atlin region, an adult female (Prov. Mus. no. 2664) taken at Wilson Creek, June 19, 1914, an immature bird (Prov. Mus. no. 2666) from Blue Cañon, August 18, 1914. The first mentioned has been recorded as *Buteo swainsoni* (Anderson, 1915, p. 12), the second as *Buteo borealis alascensis* (Anderson, *loc. cit.*, p. 11).

The two adult females collected by Brooks and myself, both in worn plumage and just beginning the annual molt, are essentially alike. They are uniformly dark-colored, almost sooty, and in each there are white markings at the base of the feathers that show through more, probably, than they would in fresh plumage. New feathers coming in are darker, more sooty, than the old, worn plumage.

In Brooks' specimen the tail is mostly dark, with scarcely a trace of red, it is mottled longitudinally with whitish, and there is a subterminal band of blackish. There are two aberrant rectrices. One has the inner web mostly white; the other is broadly barred with dusky, there is a sharply defined triangular white spot at the tip of the outer web, and the subterminal dusky band is broader than on the other feathers.

In the adult female taken by myself the exposed portions of the rectrices are dusky, mottled longitudinally with whitish and with dark markings, and there is a good deal of reddish on the terminal fourth

of the tail. There is a broad subterminal band of black, and the tip is white, suffused with reddish. The inner webs, and part of the outer webs, are white or gray, irregularly flecked with dusky. The outer rectrix (present only on the left side) has the outer web barred with blackish its entire length. Below, the tail is mostly white, with small, irregular dusky markings. On certain of the upper tail coverts is the only part of the body plumage of the bird where distinctly chestnut markings appear.

Brooks' specimen is peculiar in that but the three outer primaries are emarginate, a condition that is not supposed to exist in the *Buteo borealis* group of hawks, where the presence of four emarginate primaries has been accepted as one of the diagnostic features of the species. We examined the freshly killed bird carefully, and there is no question but that the full number of primaries was present.

The adult female in the Provincial Museum, Victoria, differs somewhat from the two just described. It is a darker colored bird even, with the concealed white markings greatly reduced in size and number. The feathers on chin, throat, and upper breast are dusky to the base. The plumage generally is not so worn as in our two birds, and there is hardly a trace of white showing through on the breast.

The tail is quite different from those of the other two adults. There is but a mere trace of rufous upon it. There is a terminal band of black, 35 mm. to 45 mm. in width (widest on the outer feathers), and above this the tail is crossed by a series of narrower bands, seven black and eight light colored, the dark colored strips becoming broader toward the base of the tail. The light colored areas are white on the inner web, grayish on the outer. The tail differs from that of the immature in the broad, black terminal band, in the lesser number of narrower bands, in the more distinctly whitish color of the paler areas, and in that it is more squarely truncate at the end. Individual rectrices are broader and more square ended than those of the young bird. The two central tail feathers of this adult are being renewed, and are about one-third emerged from their sheaths. They are of exactly the same character as the others, in interesting confirmation of the fact that this type of plumage is retained year after year. The older birds do *not* eventually acquire a red tail.

This specimen has lost one primary of the left wing, giving it an appearance of having but three emarginate primaries on that side, a condition which is probably responsible for the misidentification of the bird as *Buteo swainsoni* at one time.

The immature birds are like the adults with the exception of the tail. The tail feathers are dark sooty brown (the same color as the body plumage) on the outer web, lighter colored on the inner web, and crossed by eight or nine blackish bands. The tail pattern, essentially similar to that of immature *calurus*, differs from conditions in that form in being darker (even than in the darkest *calurus*), and in that the cross-bars are broader and fewer in number. Often, too, in young *harlani* the cross-bars tend to be U-shaped or V-shaped on individual feathers, rather than extending horizontally across. In two specimens there is a faint tinge of rufous at the tip of the tail. These hawks are generally dark colored birds but differ from even the darkest phase assumed by *calurus* (of which there are both adult and young at hand) in their sooty hue. In *calurus* there is a great deal of rich brown or chestnut in the coloration, which is altogether lacking in the Atlin birds.

In this series of specimens there is some variation, shown principally in extent of the partly concealed white markings. In the darkest colored birds the white markings in the body plumage are mostly reduced to small paired spots on feathers that are blackish over most of their area. The white markings are almost entirely concealed; the birds are almost uniformly dark. On the thighs and tibial plumes there are the merest flecks of whitish. The lightest extreme is represented by a bird with broadly white-barred thighs and tibial plumes, conspicuous bars and blotches on breast and belly, and with chin and throat mostly white.

The "soft parts" of two of the birds collected were colored as follows. No. 44730; ♂ juv. (just out of the nest): Eye stone gray; feet pale greenish yellow; bill black; cere and gape greenish. No. 44731; ♀ ad: Eye dark sepia; feet greenish yellow; bill mostly black, tinged with bluish along cutting edges; cere and gape greenish.

One fact stands out clearly; these birds are identical with the *Falco harlani* of Audubon (1830, pl. 86), which is the *Buteo borealis harlani* of the A. O. U. Check-list (1910, p. 158). Our two adults are closely similar to Audubon's plate, and they answer exactly the description of Audubon's type specimen given by Sharpe (1874, p. 191). The fact that the supposed young of *harlani* as described by Sharpe (*loc. cit*) is not at all like the young birds I collected is of no moment, for Sharpe's bird (from "Western Mexico") was not *harlani* at all. It appears to be the young of *calurus*. The same sort of mistake was made by Cassin (in Baird, 1858, p. 24) where one phase of



coloration seen in *calurus* is described as young *harlani*, a mistake that is pointed out in Baird, Brewer and Ridgway (1874, vol. 3, p. 294).

At first glance it seems startling to ascribe to the Harlan hawk a far northern breeding habitat. In the A. O. U. Check-list (1910, p. 158) the range given is as follows: "Lower Mississippi Valley and Gulf States, from Louisiana to Georgia and Florida; casual in Colorado, Texas, Kansas, Nebraska, Iowa, Illinois, and Pennsylvania." I cannot find; though, that there are definite published accounts of the breeding of *harlani* in any region whatever. Audubon's belief that the birds he shot near St. Francisville, Louisiana, had bred in that vicinity was based on hearsay. He shot his birds in November (see Coues, 1880, pp. 202-203) and had no first-hand knowledge of their nesting. Beyer, Allison and Kopman (1908, p. 442) in their "List of the Birds of Louisiana" state: "None of the writers has evidence of its breeding in Louisiana." It seems to me, in the absence of any positive published statements, that the assumption that the breeding ground of the Harlan hawk is in the Gulf states is an utter mistake.

Besides the Atlin series there are at hand three specimens of hawks from the northwest that I think are referable to *harlani*. These are two young birds (nestlings), from a point sixty miles below Forty-mile, Yukon Territory, July 28, 1894, collected by C. L. Hall (Mus. Vert. Zool. nos. 4966, 4967); and an immature male (Mus. Vert. Zool. no. 42048), a migrant, shot by the present writer in Kispiox Valley, near Hazelton, British Columbia, August 27, 1921 (see Swarth, 1924, p. 336).

These birds in life were extremely puzzling. While there was much to suggest *Buteo borealis* in the actions of the living bird, the uniformly dark coloration brought *B. swainsoni* to mind, and an occasional glimpse of white marked rectrices in a bird wheeling in distant flight was distinctly suggestive of *Archibuteo*. With specimens in hand, *Buteo swainsoni* and *Archibuteo* were quickly eliminated, of course, but other questions remained.

The status of the Harlan hawk as a distinct subspecies has been questioned. Our own findings in the Atlin region, while not assumed to be a final disposal of all the difficulties involved, do seem to place this form in a more secure position as a geographic race than it has yet enjoyed. The birds were abundant and nesting over a wide expanse of territory, and within that region they were the only form of *Buteo borealis* that was seen. Parents and young were seen together

on many occasions, and an old bird and one of its offspring were secured, probably the first time that old and young of this form have actually been collected. The young are distinctive and quite unlike the young of *calurus*, the other dark colored form of *Buteo borealis*. All this is corroborative of the theory that *harlani* is a "good" subspecies, in the sense of being a geographic race.

There is interesting evidence, of a negative sort, bearing upon the migration route of the Harlan hawk, in the fact that in our series of red-tails from the southwest, comprising about one hundred skins from California, Nevada and Arizona, there is not one specimen unequivocally of *harlani*. The only possible exception is an immature female (Mus. Vert. Zool. no. 4094) taken at Julian, San Diego County, July 27, 1908. This is a dark, blackish colored bird, like *harlani* in shade of color, but it is peculiar in lacking any of the partly concealed white spots and blotches that occur in that form. The uniformly black color of this bird may well be explained on some ground other than subspecific identity with *harlani*.

The non-occurrence of *harlani* in so large a series of specimens from the southwest is strongly suggestive of the migration route of this bird extending southeast from the breeding ground, crossing the Rocky Mountains in the far northern portion of that range. This is the route that is known to be traversed by many species that spend the summer in the extreme northwest, and what is known of the winter habitat of the Harlan hawk is corroborative of such a theory.

It is of interest to note that the red-tail (*Buteo borealis alascensis* Grinnell) of the Sitkan district, Alaska, some one hundred miles to the westward of the Atlin region, across the coast ranges, is of the same general type of coloration as *calurus*, to the southward, and shows no approach toward the characters of *harlani*.

In the light of all the foregoing facts, a revised statement of the range of *Buteo borealis harlani* might be worded as follows: Breeds in extreme northern British Columbia, east of the coast ranges, north into the valley of the Yukon, and eastward for an undetermined distance. Migrates southward east of the Rocky Mountains, through the Mississippi Valley to a winter home in the Gulf states.

While the bulk of evidence, as just given, is all corroborative of this view, there are some opposing facts that should still be borne in mind. The palest extreme of the red-tailed hawk, *Buteo borealis krideri*, has been taken in the same general region, at Eagle, Alaska, in winter (Bailey, 1916, p. 321), and on the Stikine River, breeding

(Swarth, 1922, p. 212). Bishop (1900a, p. 73) speaks of the red-tails of the Yukon region (referred to *B. b. calurus*) as being in both the light and the dark phase, about half of each, and of light colored and dark colored birds breeding together. Nothing of the sort was seen in the Atlin region, which may indicate that while *harlani* alone occurs in that section, it has a relatively limited range. I did see one pale-colored bird, apparently *krideri*, near Gladys Lake, but this was on September 7, when the southward migration was going on, and many hawks were seen passing southward overhead.

Both as regards different color phases and geographic variation, the coloration of the *Buteo borealis* group (as well as of some other species of hawks) is admittedly a difficult subject, and one that is still far from being understood by any one. The most I can claim for the facts here adduced is that they are corroborative of the idea of *Buteo borealis harlani* being a geographic race rather than a "color phase," such as is the darkest type of coloration seen in *B. b. calurus*.

These dark-colored Buteos were seen by us almost daily through the summer and in all parts of the region that we visited. On May 21 several were observed soaring low over the snow-covered slopes on the east side of White Pass. During the next week, at Carcross, they were seen daily; apparently several pairs were settled on their nesting grounds near the town.

About Atlin these hawks were distributed throughout the lowlands; there were nesting pairs at intervals of a few miles in whatever direction one traveled. Although the species was thus relatively numerous, specimens were hard to obtain; the birds were remarkably wary.

The Harlan hawk is in the Atlin region mostly a bird of the timber. The sort of perch most often chosen is the top of one of the taller spruce trees, often in fairly dense woods but always with such a commanding view as to make approach unseen out of the question. With the exception of the dark colored hawks seen in White Pass early in the season and supposed to be of this species, none was observed in the open country above timber line. The abundance of ground squirrels might have been supposed to be an attraction to that region, too. They were extremely wary always, so much so that although both birds of a pair might circle about, screaming, as long as an intruder remained in their territory, it was generally impossible to approach within gun shot.

One nest was found. It was in the valley a few miles from Atlin, in rather open spruce woods, just above a stretch of marsh land. The

nest was near the top of an isolated spruce, on a branching limb, about sixty feet from the ground. It was a huge mass of sticks, a platform that had been flattened to such an extent that the young birds were in plain sight from the ground nearby. On July 6 it held two young, with feather rows showing through the down on the breast. Returning on July 20 we found the young birds gone, but discovered them in nearby trees. They had evidently just left the nest; wing and tail feathers were not yet full grown, and they could make but short flights. On August 11 a second brood, again of two birds, was found, obviously just out of the nest. These birds could fly but feebly; when found they were on the ground in dense spruce woods. One young bird and one parent were shot.

Of the six specimens I collected four had crop or stomach or both well filled. Two contained rabbit (*Lepus americanus macfarlanei*), one held ground squirrel (*Citellus plesius plesius*) and chipmunk (*Eutamias borealis caniceps*), and one held rabbit and chipmunk.

During September, Harlan hawks were migrating in numbers. They were seen near Atlin daily, and between Atlin and Teslin (September 7 to 15) a number were observed drifting southward. On September 21, I saw two, the last observed.

### ***Aquila chrysaetos* (Linnaeus). Golden Eagle**

Seen at Carcross, May 22, and near Atlin on September 21, my last day in the field. Occasional birds were encountered throughout the summer, so the species may be assumed to breed in this general region. Restricted mostly to the mountains, where presumably the open country is more favorable to the eagle's mode of hunting than are the heavily forested lowlands.

### ***Haliaeetus leucocephalus alascanus* C. H. Townsend**

#### **Northern Bald Eagle**

One was seen near Atlin, May 29; not otherwise observed. The species has been found nesting in this region (see Anderson, 1914, p. 12).

### ***Falco rusticolus rusticolus* Linnaeus. Gray Gyrfalcon**

An important discovery was the finding of this species, to all appearances upon its nesting ground. On July 28, on the summit of Spruce Mountain, Brooks first encountered a gyrfalcon, feeding upon

a *Citellus*. Investigation showed that rock piles upon each of several commanding eminences had been used as look-out points by one or more of these falcons, evidently for a long time. The rocks were plentifully splashed with droppings, and ptarmigan feathers and other fragments scattered about told their own story. Brooks set steel traps at three places, and on July 31 he caught a gyrfalcon in one of them. It was an adult female, well started in the annual molt. Molting tail feathers produced a gap that would have been conspicuous in flight and which did not appear in the bird first seen, so there were evidently two, at least, of the species, ranging over this mountain.

On August 28 another gyrfalcon was seen on the slope of Monarch Mountain, near Atlin.

This, I believe, is the first reported summer occurrence of the species in British Columbia. Atlin is far south of any previously known breeding station in western North America. In all likelihood, though, the gyrfalcon will be found nesting some distance still farther south, on the high Alpine-Arctic plateau that covers so much of north-western British Columbia.

#### ***Falco peregrinus anatum* Bonaparte. Duck Hawk**

Of rare occurrence. Single birds were seen on Tagish Lake, May 27, near Atlin, June 29, on Spruce Mountain, August 8, and at Lake Teslin, September 12. ~

#### ***Falco columbarius suckleyi* Ridgway. Black Pigeon Hawk**

No pigeon hawks were seen until the southward migration had begun. First noted August 11, when two were observed at different times. From then on until September 21 (the last date of record) an occasional bird was seen at long intervals, probably not more than ten or twelve, all told.

It was distinctly surprising that the two specimens collected should prove to be typical examples of the subspecies *suckleyi*. Besides these two, another, not collected, was observed through binoculars at close enough range to establish its identity also as *suckleyi* without a doubt. The other pigeon hawks seen were at too long range to permit of subspecific determination. The two birds collected were an immature male, shot in the town of Atlin on August 15 (no. 44736), and an adult female, in the midst of the annual molt, shot on August 28 (no. 44737).

The breeding range of *suckleyi* is, I believe, unknown, but it has been assumed to be along the coast and farther south than is indicated by the occurrence of these migrants in the Atlin region. The northernmost record of the subspecies prior to this was, I believe, from the upper Skeena Valley, British Columbia (Swarth, 1924, p. 337).

That *Falco columbarius columbarius* also occurs at Atlin is proved by a specimen in the Provincial Museum, Victoria, collected there August 13, 1914 (Anderson, 1915, p. 12). I have seen this bird and it is unquestionably of the subspecies *columbarius*.

### ***Cerchneis sparveria sparveria* (Linnaeus). Sparrow Hawk**

Fairly common and of rather general distribution. The sparrow hawk occurs in the more open country in the lowlands, and also above timber line; it usually avoids the denser woods. Present at Carcross when we arrived the latter part of May. The last bird I saw was at Gladys Lake, September 8, but the species has been recorded from Atlin as late as September 18 (Kermode and Anderson, 1914, p. 19).

### ***Pandion haliaëtus carolinensis* (Gmelin). Osprey**

Seen about Lake Atlin at rare intervals during the summer, and at Gladys Lake, September 7. Has been found nesting near Atlin (Anderson, 1915, p. 12).

### ***Bubo virginianus subarcticus* Hoy. Arctic Horned Owl**

#### ***Bubo virginianus lagophonus* Oberholser. Ruddy Horned Owl**

Six horned owls were collected as follows: an adult male, June 5 (no. 44738); an adult male, and male and female in post-juvenal molt, July 3 (nos. 44739-44741); adult male in annual molt, August 4 (no. 44742); adult male, August 25 (no. 44743). These birds are puzzling in appearance, but, although I cannot assume to have interpreted their peculiarities beyond possibility of mistake, they seem to me to demonstrate with fair certainty that the breeding horned owl of this section is the subspecies *subarcticus*. I had expected to find *lagophonus* in the Atlin region, as the ascribed range of that subspecies includes this section, but four of the six specimens cannot possibly be considered as of that race. Nos. 44739, 44740, 44741, 44743, are extremely gray-colored birds, with perhaps the minimum of rufous in their coloration that is seen in horned owls from any section. No. 44743 has legs and toes gray-barred; in the other three, those parts

are mostly white. Altogether, the black-and-white appearance of these owls is in striking contrast to the tawny-colored *lagophonus*, as represented by a series from the upper Skeena Valley, British Columbia. Nos. 44739 and 44740 are two juvenals, taken with the male parent (no. 44741). The two young are quite unlike, one being much darker than the other; the pale colored bird is the more rufescent of the two.

Two specimens were collected that are like *lagophonus* from the Skeena Valley. One of these (no. 44738, adult male, June 5) with hardly a doubt was not a breeding bird. Of the second (no. 44742, adult male, August 4) it cannot be said with any certainty whether or not it had bred in the region. These two individuals may be, as their appearance indicates, examples of *lagophonus* that had wandered beyond the usual confines of that race. The breeding birds in the series are most nearly like specimens of *subarcticus* from the Yukon region, a short distance to the northward. The Atlin region forms the southern boundary of the Yukon drainage, and it is to be expected that the distribution of some Yukon species should be co-extensive with this drainage system.

Horned Owls were fairly common in the Atlin region; hooting could be heard almost every night. One bird was seen at Lake Teslin, September 12. Of the six horned owls collected, four had their stomachs filled with remains of rabbits. Those of the other two were empty.

### ***Surnia ulula caparoch* (Müller). Hawk Owl**

On May 29 a hawk owl was found in a tract of spruce timber at the northern base of Monarch Mountain, and as the bird was seen subsequently at the same place on several occasions, it may have been nesting there. This was the only one seen until the end of the summer. On August 19 Brooks shot a young bird, in first winter plumage throughout save for remnants of down about the head, and from then on others were seen at frequent intervals.

The three birds collected, two by Brooks, the other by myself (no. 44744, male, September 19), are alike and are extremely dark colored. Compared with a large series from northern Alaska, the Atlin specimens are more slaty above and less reddish below. These color differences cannot be explained as illustrating seasonal change or sexual or age variation, but neither can they with any certainty be correlated with any geographic area.

One hawk owl had in its stomach the remains of a *Peromyscus*.

**Ceryle alcyon caurina** Grinnell. Western Belted Kingfisher

There appeared to be a few pairs of kingfishers nesting in the region about Atlin. The species was far from common but an occasional bird was seen throughout the summer.

**Dryobates villosus leucomelas** (Boddaert)

## Northern Hairy Woodpecker

Only three hairy woodpeckers were encountered during the summer, one seen July 6, a male collected on July 7 (no. 44745), and a male collected on August 22 (44746). The two specimens, collected near the town of Atlin, are unquestionably of the subspecies *leucomelas*, here near the southern limit of that race. In the upper Stikine Valley, 150 miles south of Atlin, the subspecies *monticola* occurs, in fair abundance (Swarth, 1922, p. 217). In the *monticola* series at hand from that region there are specimens that show intergradation toward *leucomelas*.

**Dryobates pubescens nelsoni** Oberholser. Nelson Downy Woodpecker

An adult male downy woodpecker (no. 44747), shot near Atlin, June 8, was the only one of the species that was seen. This bird is referable to the subspecies *nelsoni*. It has slightly more black marking on the outer rectrices than is seen in specimens of *nelsoni* from the Yukon, but in all other respects it appears to be typical of that race.

**Picoides americanus fasciatus** Baird. Alaska Three-toed Woodpecker

Unexpectedly rare. The first was seen July 11; afterward perhaps five or six, all told, were encountered. One seen at Lake Teslin, September 11. One specimen collected, an adult female, July 11 (no. 44748).

**Colaptes auratus borealis** Ridgway. Boreal Flicker

Present at Carcross when we arrived, May 22, and at Atlin when we reached there a few days later. Breeds in fair abundance throughout the lowlands. A nest hole, partly finished, was found May 31, in a stump in a clearing, one foot from the ground. On June 24 a flicker was seen feeding young in a hole in a dead poplar about three feet



from the ground. Other nests were found, similarly placed, low down in dead timber. The last flicker was seen September 5.

Two specimens were collected (nos. 44749-44750), a female on August 17, a male on August 22.

***Chordeiles virginianus virginianus* (Gmelin).** Eastern Nighthawk

The first nighthawk arrived at Atlin on the evening of June 12; the species was fairly common thereafter in the lowlands. During the last two weeks in August the southward migration was under way, and every evening the birds could be seen passing by, all going in the same direction. Last seen on the evening of September 6. Two specimens collected (nos. 44751-44752), both females, taken on August 12 and 20, respectively.

***Selasphorus rufus* (Gmelin).** Rufous Hummingbird

Seen on only three occasions, on June 11, June 13, and July 12, all within a few miles of the town of Atlin. One of the three was an adult male, hence easily recognizable, the others were inferentially of the same species.

• ***Sayornis sayus yukonensis* Bishop.** Northern Say Phoebe

Present at Carcross upon our arrival, May 22. Breeds in the town of Atlin, and scattered pairs occur elsewhere, usually about abandoned buildings. The southward migration of this species was under way after the middle of August. On August 24, near the summit of a high mountain, a Say phoebe, first observed perched upon a rocky pinnacle, was seen starting southward, ascending higher as the mountain was left behind, the beginning of what was to be, apparently, a long flight. The last Say phoebe was seen at Lake Teslin, September 10.

I collected three adults (nos. 44753-44755) and Brooks collected others, and these, together with additional northern specimens in this museum, bear out the validity of the subspecies *yukonensis* (Bishop, 1900, p. 115). The northern bird has a slightly smaller bill than the southern race; otherwise, differences of measurements between the two are of slight moment. The color differences, however, are readily apparent, both in the juvenal and adult plumages, *yukonensis* being clearer gray where *sayus* is brownish or rusty, as described by Bishop (*loc. cit.*).

## MEASUREMENTS IN MILLIMETERS OF SAYORNIS SAYUS SAYUS AND S. S. YUKONENSIS

| No.  | Sex | Locality                    | Date          | Wing         | Tail        | Culmen      |
|--|-----|-----------------------------|---------------|--------------|-------------|-------------|
| 4594   | ♂   | Forty-mile, Yukon Territory | May 5, 1901   | 107          | 86          | 14          |
| 44755  | ♂   | Atlin, British Columbia     | June 11, 1924 | 105          | 84          | 14          |
| —*   | ♂   | Atlin, British Columbia     | June 17, 1924 | 99           | 78          | 14          |
| 44753  | ♀   | Careros, Yukon Territory    | May 24, 1924  | 98           | 78          | 13          |
| 44754  | ♀   | Careros, Yukon Territory    | May 25, 1924  | 97           | 78          | 13          |
| —*   | ♀   | Careros, Yukon Territory    | May 24, 1924  | 98           | 77          | 14          |
| Average, minimum and maximum of 10 breeding males from California and Nevada |     |                             |               | 102.4        | 79.9        | 15.4        |
| Average, minimum and maximum of 5 breeding females from California           |     |                             |               | (98 0-104 0) | (77.0-83.0) | (14.5-16 0) |
|  |     |                             |               | 97.0         | 76.6        | 14.9        |
|  |     |                             |               | (91 0-101 0) | (73 0-80 0) | (14.0-16.0) |

\* Coll Allan Brooks.

**Nuttallornis borealis** (Swainson). Olive-sided Flycatcher

First seen at Carcross, May 26. Summer visitant to the Atlin region in small numbers. An occasional pair was nesting at wide intervals throughout the surrounding lowlands. In August, when the southward migration had begun, the birds were more frequently seen. Last noted August 28. One specimen was collected, an adult male taken June 2 (no. 44756).

**Myiochanes richardsonii richardsonii** (Swainson)

## Western Wood Pewee

Present at Carcross, May 22. About Atlin the species was fairly common throughout the lowlands. Last seen August 28. Three specimens were collected, two adults and one juvenile (nos. 44757-44759). There are at hand twelve additional specimens from northern localities, from the Skeena River and the Stikine River, British Columbia, and from the coast of southeastern Alaska, and judging from this series I can see no justification for recognition of the subspecies *saturatus* (of Bishop, 1900, p. 116). These birds are to my eye indistinguishable from more southern specimens.

**Empidonax traillii alnorum** Brewster. Alder Flycatcher

Arrived at Atlin on June 12. Not common, but found in willow-grown swamps throughout the lowlands. Last seen August 29. Three specimens were collected, two adults and one immature in first winter plumage (nos. 44760-44762).

**Empidonax hammondii** (Xantus). Hammond Flycatcher

Fairly abundant in the lowlands of the Atlin region throughout the summer. Arrived on June 1, and was last noted August 31. Three specimens were collected (nos. 44763-44765), an adult male on June 3, a female in winter plumage throughout on August 21, and a male still in juvenal plumage on August 24.

**Empidonax wrightii** Baird. Wright Flycatcher

Three specimens were collected (nos. 44766-44768): an adult male at 3000 feet altitude on Monarch Mountain, June 22, an adult female

at 3500 feet on Otter Creek, July 30, and a male in juvenal plumage at the base of Monarch Mountain, August 17, the last date of record.

The Wright flycatcher was of decidedly rare occurrence, not more than six or eight individuals, all told, being seen during the summer. Breeding birds were taken at a higher altitude than that at which *hammondi* occurs.

**Otocoris alpestris arcticola** Oberholser. Pallid Horned Lark

Breeds in fair abundance throughout the open country on the ridges above timber line. On June 19, young out of the nest were seen. During the last week in July and the first week in August, old and young were in the midst of the molt; two adult males collected on August 7 and 8, respectively, have nearly completed the change. During this season of molt, the horned larks were generally found either as single birds or two or three together, but before the end of August they were gathered in flocks of from fifty to one hundred individuals.

Fourteen specimens were collected (nos. 44769-44782), three in juvenal plumage, three adults in worn breeding plumage, and one immature and seven adults in more or less completely acquired winter plumage. The species was last seen on August 24, though later trips were made to the high altitudes where it occurs.

**Pica pica hudsonia** (Sabine). American Magpie

Several pairs were seen near Carcross during the last week in May, and two nests found, occupied but without eggs. None was seen about Atlin during the early part of our stay, and we were told that magpies did not nest in that section but that the birds did appear there at the very end of the summer. I saw several at Gladys Lake, September 8. On September 19 one appeared at Atlin, and I saw the species each day until the 23rd, when I left.

The late summer invasion of the Atlin region by the magpie is probably related to the migration of this species to the coast of southeastern Alaska, as observed by me on the lower Taku River in September, 1909 (Swarth, 1911, p. 77). The valley of the Taku, lying southwest of Lake Atlin, is a natural outlet from this region to the coast, and the magpies I saw there were, together with other species, migrating down this valley from the interior.

***Perisoreus canadensis canadensis* (Linnaeus). Canada Jay**

Fairly common, both at Carcross and about Atlin. At the time of our arrival, during the last week in May, old and young together were roving through the woods in small bands, apparently family groups. During July both old and young were going through the molt; specimens of adults and young collected on August 14 had completed the change. Seventeen specimens were collected (nos. 44783-44799), including three summer adults (two from Carcross), seven in juvenal plumage, and seven adult and immature in fresh winter plumage.

***Corvus corax principalis* Ridgway. Northern Raven**

This is another species that appears in the Atlin region in the fall. Kermode (1914, p. 21) found it common there during September, 1913 (recorded as *Corvus caurinus*). Seen by me on just one occasion, at Lake Teslin, September 12, when two birds appeared, attracted by refuse from the carcass of a moose that was being cut up.

***Euphagus carolinus* (Müller). Rusty Blackbird**

One bird seen at Carcross, May 24, but the species had probably arrived some time before. Upon our arrival at Atlin a few days later we found scattered pairs established in most of the little swamps that are distributed throughout the lowlands. Small flocks of young appeared in July, but the species was not abundant at any time, and most of the birds had gone by the middle of August. I saw a few at Gladys Lake, September 8 and 9, the last I encountered, though Kermode (1914, p. 21) has recorded it from this region as late as September 19.

***Carpodacus purpureus purpureus* (Gmelin). Eastern Purple Finch**

On June 25, near the town of Atlin, I heard a purple finch utter a few notes of its song, and on June 28, at the same place, I collected an adult male (no. 44800). This constitutes, I believe, the extreme northwestern point of record for this species.

***Loxia leucoptera* Gmelin. White-winged Crossbill**

First seen on June 3, a single bird. Increasing numbers arrived daily, until by the middle of June flocks of fifty or sixty birds

appeared. By the last week of June the crossbills were in pairs, apparently preparing to nest, but soon after their numbers lessened until relatively few remained. Two specimens were collected, both adult males (nos. 44801-44802).

***Spinus pinus* (Wilson).** Pine Siskin

Arrived at Atlin toward the end of June. First noted June 25, and became fairly numerous by the middle of July. At the time of my departure, September 23, siskins were still present in numbers.

***Calcarius lapponicus alascensis* Ridgway.** Alaska Longspur

At Carcross, May 23, the cat at the hotel where we stayed brought in a longspur, which we were able to identify from the feathers scattered about. This, presumably, was a belated north-bound migrant. The species was next encountered on September 1, when I flushed several high upon the mountain above "Blue Cañon." On September 7 several large flocks were observed between Surprise and Gladys lakes.

***Passerculus sandwichensis alaudinus* Bonaparte.**

Western Savannah Sparrow

When we reached Atlin, May 28, Savannah sparrows had already arrived, and the male birds could be seen singing from low perches in the more open swamp-land. The species was not common, but a few pairs were scattered through the wet meadows that partly encircle the town of Atlin, and small numbers were seen elsewhere, where suitable conditions obtained. On June 25 a nest was found, containing six eggs on the point of hatching. The nest was sunk in the ground, in marsh grass, with no trees or bushes in the near vicinity.

On September 1, Savannah sparrows were seen in numbers, migrating, on some of the higher, more open, mountain slopes. The last bird was seen September 21. Three specimens were collected, an adult male, and male and female in first winter plumage (nos. 44803-44805).

***Zonotrichia gambelii* (Nuttall).** Gambel White-crowned Sparrow

An abundant summer visitant to the lowlands of this region. At Carcross when we arrived, May 22, the Gambel sparrows were already paired and preparing to nest. The first nest was found at Atlin on

May 31, containing two eggs; on June 4 it held a set of four. Other nests were found on June 11, with four eggs (no. 1983), and on June 12, with five eggs (no. 1984). These were all essentially alike in structure and location. They were on the ground in rather damp meadow land, in fairly open areas interspersed with thickets of willow and dotted with tiny wild rose plants. The nests were well hidden under tufts of grass, willow shoots, or roses.

One (no. 1983) measures 120 mm. outside diameter, 65 mm. inside diameter, 40 mm. inside depth. The outer walls are mostly shreds of bark and coarse (dry) grass stems, the lining is of fine grass and a little horse hair.

Another nest (no. 1984) measures 110 mm. outside diameter, 65 mm. inside diameter, 35 mm. inside depth. The outer walls are mostly shreds of bark, the lining is of fine grass and a little mammal hair, mostly dog and mountain sheep (taken from a nearby carcass of the first, and scraps of hide of the second).

On June 25 the first young birds appeared, but although the species was common, relatively few spotted young were seen at any time. The birds nested in fair abundance in gardens in the town of Atlin, and in waste land between the houses, and more young birds were seen there than elsewhere. On July 11 the first juvenile was collected showing beginnings of the post-juvenal molt, which, roughly, continues through the month of July. On August 6 a young male was taken, still with many pinfeathers but with none of the juvenal plumage left. By August 14 the young birds were practically through the post-juvenal molt. Adults at that date were nearly all stubby-tailed. A young female collected August 24 is in perfect first winter plumage.

During the breeding season the Gambel sparrow was confined to the lowlands, but soon after the beginning of the post-juvenal molt there was a scattering of old and young that took many individuals high up into the mountains. There they formed loosely connected flocks in company with the golden-crowns, the beginning of an association that in California we see carried on throughout the winter.

On August 29 the species was still abundant. It was last noted on September 5, but as a number of the birds were seen on that date, some probably lingered several days longer. Careful search on September 19, however, failed to disclose a single one.

Sixteen specimens were collected (nos. 44806-44821), fourteen in juvenal plumage or in various stages of the post-juvenal molt, and two in first winter plumage.

I am using the binomial name for this bird in the conviction that the three white-crowned sparrows, *leucophrys*, *gambelii*, and *nuttalli* are three distinct species. There are various trenchant external characters of plumage and other parts distinguishing them, there are just

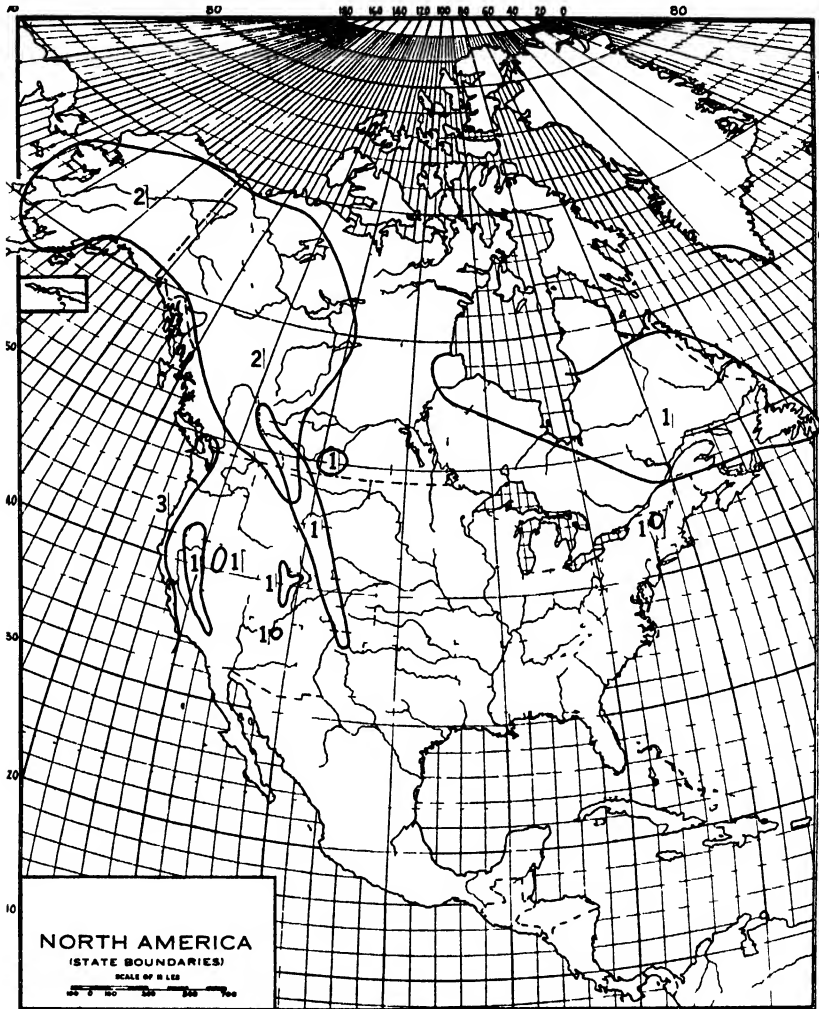


Fig. J. Map showing breeding ranges, approximately outlined, of (1) *Zonotrichia leucophrys*, (2) *Zonotrichia gambelii*, and (3) *Zonotrichia nuttalli*.

as notable differences of song, and the breeding ranges and migration routes also are indicative of specific differences (see fig. J). As regards external characters, while I am aware that there are various published statements of the existence of intergradation between these forms, these



assertions are all rather vague. In this museum there are approximately 200 specimens of *leucophrys*, 270 of *gambelii*, and 200 of *nuttalli*. There is not one equivocal specimen in this series, not one that can be said to illustrate in even the slightest degree intergradation between any of the forms. Nor have I seen intermediates in other collections. If any such do sporadically occur it seems to me that they should be regarded as hybrids rather than geographic intergrades. Riley (1912, pp. 66-67) has given conclusive evidence as to conditions at the one place where the ranges of *leucophrys* and *gambelii* are known to abut. Each retains its specific identity. As far as I know, the breeding range of *nuttalli* is widely separated both from that of *leucophrys* and of *gambelii*.

The different songs of these three birds also is something that cannot fail to impress one. When in addition to the consistently uniform external characters found in each form, there are also such differences of song and breeding ranges as are seen, it seems to me that every condition is met whereby they should be accorded specific rank.

#### LIST OF FORMS OF THE WHITE-CROWNED SPARROWS OF THE GENUS ZONOTRICHIA

1. *Zonotrichia leucophrys* (J. R. Forster). Eastern White-crowned Sparrow.
2. *Zonotrichia gambelii* (Nuttall). Gambel White-crowned Sparrow.
3. *Zonotrichia nuttalli* Ridgway.~ Nuttall White-crowned Sparrow.

#### *Zonotrichia coronata* (Pallas). Golden-crowned Sparrow

There is a small and yearly diminishing list of North American birds, the breeding habits of which are almost or quite unknown, and the golden-crowned sparrow has been one of the few passerine species included in that category. It is true that many years ago detailed accounts were published professing to give particulars of the nesting of this bird, but those were cases of mistaken identification and so far as I know there has not yet been printed any unquestioned account of the breeding of the golden-crowned sparrow. I was, indeed, under the impression for a time that nests and eggs taken by Major Brooks and myself in the Atlin region were the first authentic sets to be collected, but, as I learned, there are sets in the collection of Colonel John E. Thayer, Lancaster, Massachusetts, that were taken some years ago. Through the courtesy of Colonel Thayer details regarding these sets are given below.

The old records by Heermann (1859, p. 48) and by Brewer (1878, p. 48), the former describing the nesting of the golden-crowned sparrow near Sacramento, California, the latter, in Shasta County, California, were mistakes that are obvious enough to us at the present

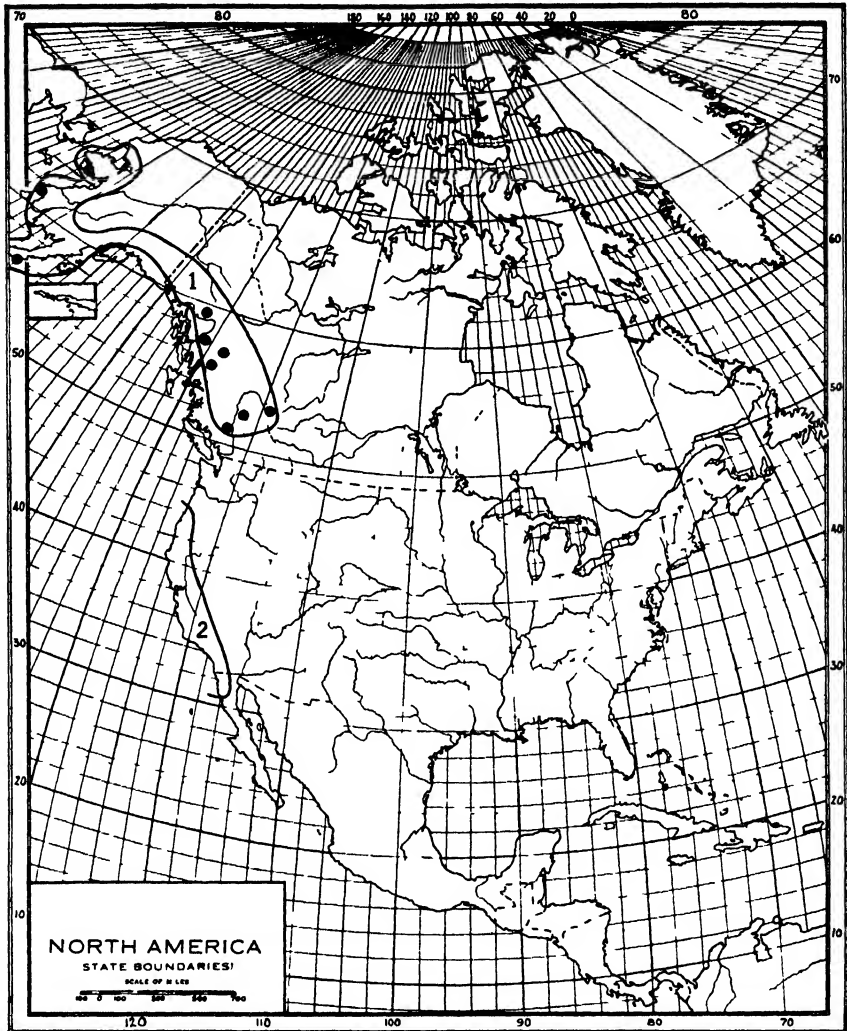


Fig. K. Map showing distribution of the golden-crowned sparrow (*Zonotrichia coronata*), with (1) breeding range and (2) main winter habitat approximately outlined. Symbols within the outlined breeding range indicate localities where the species has been found actually breeding.

time, but they were accepted at face value for many years. Their widespread repetition created an impression that the nest and eggs of this bird were well known, an impression that persisted long after

those records were specifically discredited. The only other published accounts bearing upon this subject that I have seen are by Bishop (1900, p. 85), who describes an unfinished nest found in White Pass; and by Osgood (1904, p. 75), who casually mentions "several" nests found at Ibanina Bay, Alaska Peninsula, the latter part of June, containing from four to six eggs each.

I, myself, had been twice before on the nesting grounds of the golden-crowned sparrow, and the fact that I had failed to find nests then spurred me on to renewed efforts on this third opportunity. In British Columbia this bird is a summer visitant at high altitudes, nesting above the limit of upright timber. In the Atlin region it is so closely restricted to the heights that I did not see even a migrant in the lowlands.

On May 29 we made our first climb above timber line, to the top of Monarch Mountain, some 4500 feet altitude, about three miles south of Atlin. The golden-crowned sparrows had arrived and were singing from the tops of the balsam thickets, but no nest building was detected. This mountain top, as it proved, was peculiarly adapted to the needs of this species. At least there were more of the birds here within a relatively limited area than we saw anywhere else. Long stretches of rolling hilltops, grass-covered for the most part, were interspersed with scattered thickets of prostrate or stunted balsam, and with larger areas of trailing birch. This birch was in most places not over knee high and easily walked over. Little lakelets occupied some of the hollows, and from them small streams flowed part way down the mountain. Lakes and streams both were almost or entirely dry before the summer was over.

On June 19 we returned to this same summit, to make a thorough search for nests. A general notion that these would be in the balsams, as the most effective cover in sight, led us first to direct our attention to these thickets, the more so as they formed the singing perches of the male birds. Half an hour's search brought no results other than the discovery of old robin nests, so the balsams were abandoned for the time. A little later, as I was traversing a dry, open ridge, ploughing through a mat of birch, a sparrow darted out some eight or ten feet away, not to fly, but to scuttle, mouse-like, along the ground under the sparse, sprawling branches. A brief search disclosed the nest (see pl. 7, fig. 6). A ledge of rock protruded a few inches from the ground in the center of the thicket, and the nest was sunk against this shelter, fairly well concealed by the vegetation above. There were five eggs,

incubated about one-half. Within a few hundred yards a second nest was found in a similar situation, on the ground under some trailing birch, with four eggs incubated as the first lot were. Again the bird was seen running from the nest under the bushes.

The first nest was built externally of gray plant fiber, a few balsam twigs, bits of dried flakes of bark, and a very little green moss; the lining was of dry grass, with several white ptarmigan feathers interwoven. External diameter, 120 mm.; internal diameter, 65 mm.; outside depth, 55 mm.; inside depth, 35 mm.

The second nest differs in minor details, having far more green moss worked into the outer wall, and lacking any feathers in the lining. External diameter, 135 mm.; internal diameter, 65 mm.; outside depth, 55 mm.; inside depth, 35 mm.

The two sets of eggs measure, in millimeters, as follows:

First set (no. 1986); 22.0 x 15.8, 22.2 x 16.2, 22.2 x 15.5, 23.0 x 16.0, 22.0 x 16.0.

Second set (no. 1985), 23.5 x 16.2, 24.0 x 16.0, 23.0 x 16.5, 22.8 x 16.5.

The eggs are speckled and mottled with brown on a pale greenish ground. Of the two sets here described, one (no. 1986) is much more heavily marked than the other, the ground color being almost obliterated. The eggs of the golden-crowned sparrow are closely similar to those of the Gambel and Nuttall sparrows. Both of the above described sets can be duplicated almost exactly in series of eggs of those species.

Several hours after our first two discoveries, Brooks found a third nest, this one in a low thicket of balsam, a thicket about twenty feet square but with the sprawling branches rising not more than knee high above the ground. The nest was in the branches, about ten inches up, and was much bulkier than those on the ground. It was a gray-colored structure, the outer walls of coarse weed stalks and shredded stuff that appeared to be the bark of some of the annuals growing thereabout. The lining was mostly fine grass, with one conspicuous white ptarmigan feather. The whole nest was about 180 mm. in diameter, and 90 mm. deep. The nest cavity was 76 mm. across. It contained four fresh eggs.

On June 22 a fourth nest was found on the same mountain, in much the same situation as the first two (see pl. 7, fig. 7). It was on a dry ridge under a scant growth of dwarf birch, the nest buried between tufts of long, dry grass, and itself constructed mostly of dry grass and

plant fiber, the lining of fine grass. It contained four slightly incubated eggs. This nest, like the others, was found by flushing the bird. The last two nests discovered, both taken by Brooks, are now in the collection of Colonel John E. Thayer, Lancaster, Massachusetts.

The dates on which these nests were taken is probably indicative of the usual time of egg-laying, but some sets are evidently laid at a much later date. On August 3, on Spruce Mountain, a pair of birds was seen, which, from their actions, obviously had a nest nearby, and on August 5, on the same mountain, a nest was found containing naked young, probably about a week old.

The Thayer collection contains four sets of eggs of the golden-crowned sparrow, collected by John Koren, with data as follows:

- (1) Anvil Mountains, near Nome, Alaska; June 21, 1910; 5 eggs.
- (2) Anvil Mountains, near Nome, Alaska; June 21, 1910; 7 eggs  
(3 broken).
- (3) Nelson Island, Bering Sea, Alaska; July 3, 1910; 3 eggs.
- (4) Shumagin Island, Alaska; July 8, 1911; 5 eggs.

The parent birds of each set are also in the Thayer collection.

On July 8 young out of the nest were first seen on Monarch Mountain, and here, as in previous experiences, I had impressed upon me the extreme wariness of the young birds. They were in thickets of dwarf birch and balsam. When a brood was flushed they scattered to distant points, and each bird, alighting in a bush, at once scuttled through and was away to another hiding place. The adults are not hard to approach; they apparently watch and direct the retreat of their offspring.

On July 18 young were taken in juvenal plumage throughout and with full-grown rectrices. Others molting into first winter plumage were collected July 27 and August 5. One young bird still mostly in juvenal plumage was taken August 24.

The young of the golden-crowned sparrow is generally similar to the same stage in the three species of white-crowned sparrows. *Coronata* lacks the decided head markings that are seen in the juvenal white-crowns and it has a suggestion of yellowish upon the forehead. Compared with the grayish *leucophrys*, young *coronata* is generally darker colored and the ventral streaks are darker, heavier, and more extensive. Compared with *gambelii*, young *coronata* is generally browner. Young *coronata* and young *nutalli* are closely similar in

body coloration, but the former is slightly darker colored as a rule. *Coronata* has a heavier bill than the white-crowned sparrows, and this character is apparent in the young birds.

The accompanying illustration (pl. 4) was made from studies of the freshly killed bird. The yellowish tinge to the lower parts, as there shown, is an evanescent color that soon disappears from the study skin. Color of bill and feet in the picture is, of course, as those parts were in the living bird.

On September 5 I made my last climb to the summit of Monarch Mountain, and on that day but a single golden-crowned sparrow was noted, the last for the season.

In all, I collected six specimens of the golden-crowned sparrow (nos. 44822-44827), as follows: one adult female (with the first set of eggs), two males in juvenal plumage, and three birds in various stages of the post-juvenal molt.

### ***Spizella monticola ochracea* Brewster. Western Tree Sparrow**

An abundant summer visitant in the region at an altitude higher than the town of Atlin. Tree sparrows may appear in the lowlands upon their advent in the spring, but when we arrived, at the end of May, they were already established on their nesting ground and we saw none in the valley. We found them in abundance at the head of Cañon Creek (from 3500 to 4500 feet altitude) and in somewhat similar surroundings at the same elevation on upper Otter Creek. In each place they occurred where willow is the prevailing tree growth, ranging in size from scrubby, mat-like thickets that can be walked over, to tangled bushes ten feet high or more. The tree sparrows were practically always found in or about the willows.

On June 30 tree sparrows appeared to be carrying food to young in the nest; by the last week in July the young were going through the post-juvenal molt. During September a few migrating tree sparrows appeared in the lowlands. Single birds were seen at Lake Teslin, September 12, and near Atlin on September 19 and 21. Eleven specimens were collected (nos. 44828-44838), two adult females in worn breeding plumage, eight young (July 30 to August 6) in various stages of the post-juvenal molt, and one immature female in first winter plumage.

***Spizella passerina passerina* (Bechstein). Eastern Chipping Sparrow**

Seen at Carcross, May 22. In the Atlin region this is a fairly common species in the lowlands. It probably does not nest on the higher mountain slopes, but at the end of the summer there was a slight movement toward higher altitudes. In the upper part of Otter Creek, up to about 4500 feet altitude, chipping sparrows were fairly common at the end of July and during the first week in August. The last chipping sparrow was seen August 24, near Atlin. Three specimens were collected (nos. 44839-44841), two adult males and one male in juvenal plumage.

***Spizella taverneri* Swarth and Brooks. Timber-line Sparrow**

The discovery of this species (see Swarth and Brooks, 1925, p. 67) was one of the most interesting of the season's results. In general appearance *Spizella taverneri* resembles *Spizella breweri* closely enough that we could not be sure in the field that it was not *breweri* that we had found, but the known range of *breweri* was so distant, and the conditions surrounding this bird were so widely different from those in the habitat of *breweri*, as to arouse our strong interest.

We first encountered the timber-line sparrow on July 8, near the summit of Monarch Mountain, about 4500 feet altitude. The surroundings there are such as obtain generally above timber line in this region, the country being open, grass covered for the most part, the damper portions with small areas of false heather and the whole interspersed with clumps of scrubby balsam, mostly prostrate, but sometimes ten or fifteen feet high. It was a raw day, with showers at frequent intervals, the rain driving before a sharp wind, conditions such as to render a search for small birds difficult and unproductive. We were following a flock of horned larks when two sparrows appeared, perched upon a balsam thicket some distance away and jerking their tails nervously. Their appearance did not accord with anything we knew in the region, and Brooks started at once in pursuit. With some difficulty, for the birds were wary, he secured one of them. This proved to be an adult female with a denuded abdomen, indication that she was, or had been, incubating eggs.

The species was next encountered in the upper part of Otter Creek, at about 3500 feet altitude, and on the surrounding mountains up to their summits, nearly 5500 feet altitude. In Otter Creek Valley

these birds were not seen along the wet bottom lands, but they frequented the dry hillsides, where the trailing birch afforded the cover they favored the most. They were at all times wary and hard to approach, far more so than most small birds, and in contrast to the actions of the several species of *Spizella* and *Zonotrichia* with which they were associated.

During the last week in July and the first week in August, spotted young were seen being fed by their parents, but mostly the young were larger, undergoing the post-juvenal molt. The species might easily be overlooked, for besides their habitual wariness the birds are with difficulty dislodged from the sheltering cover they frequent. If flushed at a distance from the tops of the balsam thickets on which they often perched when suspicious of danger (and they rarely permitted a near approach), the timber-line sparrow might easily be overlooked amid the tree sparrows, chipping sparrows, and even the *Zonotrichias*, which were in the same surroundings and arising from the bushes near at hand. When flushed they flew long distances, to dive into birch thickets, tangled masses of shrubbery about waist high, and it was rarely that a bird could be dislodged from such a refuge. They ran beneath the shrubbery, to take flight at some distant point, and such tactics, repeated over and over again, inevitably left the person in pursuit floundering clumsily through entangling branches far behind.

So, although the species was really abundant in some places, such as on certain of the higher slopes of Spruce Mountain, we secured relatively few specimens.

Together, we collected twenty-three skins, as follows: adult male, 3; adult female, 4; immature, first winter plumage, 4; juvenal, 6; molting from juvenal to first winter, 6. Fifteen of these (nos. 44842-44856) came to the Museum of Vertebrate Zoology. Two of this series have since been deposited in the United States National Museum.

### ***Junco hyemalis connectens* Coues. Cassiar Junco**

Thirty-five specimens of junco were collected (nos. 44857-44891), sixteen breeding adults (thirteen of these from Carcross), the remainder comprising some streaked juveniles and adults and immature in fall plumage. I am listing these all as of the subspecies *connectens*; but there are equivocal specimens in the series (among migrants collected toward the end of the summer) that would fit as readily into a series of *hyemalis*.



Breeding juncos from Carcross show a distinct approach to the subspecies *hyemalis*, as compared with *connectens* from the Stikine region, so much so that Carcross may be regarded as near the northern limit of the range of *connectens*.

At Carcross, May 22, male juncos were singing from the tops of bushes and small trees. Females collected during the next few days had their sets partly laid. Two nests, each with four fresh eggs, were found near Atlin, May 31. These and other nests subsequently found were all very much alike. They were all in fairly open bottom land, on the ground, and well concealed in sheltering grass and other vegetation. Juncos bred most abundantly in the lowlands, but on June 30 I found a nest with five fresh eggs on a mountain side at about 3500 feet altitude. The situation was a warm, south-facing slope; the nest was buried in a dense clump of bear-berry and grass.

On June 26 the first young out of the nest was seen, and from then on through August spotted young were fairly common in small flocks throughout the lowlands. During September juncos were migrating through the region. The last were noted September 19, but from the number seen that day I am sure that some must linger to a much later date.

***Melospiza lincolni lincolni* (Audubon). Lincoln Sparrow**

Breeding in fair abundance in the disconnected marshy areas that occur throughout the lowlands. On June 14 a nest was found with five eggs at the point of hatching. The first young was seen flying on July 2. The species was last noted on August 29. Two specimens (nos. 44892-44893) collected by myself, and others taken by Brooks, are all typical of the subspecies *lincolni*.

***Petrochelidon lunifrons lunifrons* (Say). Cliff Swallow**

Nests were seen on buildings at Carcross. The first cliff swallow was noted there on the evening of May 26, some days after our own arrival, and when we reached Atlin, May 28, the species was present in force. It nests in some numbers in the town, but we found it breeding nowhere else. The last cliff swallow was noted August 16.

***Hirundo erythrogaster* Boddaert. Barn Swallow**

This species arrived at Carcross on the morning of May 26. Old nests were seen on several houses there. It was abundant in the town of Atlin, but was not found nesting elsewhere. Last noted September 1.

E. M. Anderson (1915, p. 15) has described the nesting of a pair of barn swallows on a passenger coach that traverses the two-mile portage at Taku. The birds still rear their broods in the same place. For their convenience a box is affixed near the roof of the coach within (the sides of the car are open), and year after year the box is occupied. The coach travels back and forth across the portage several times a week, filled with people, throughout the nesting period.

***Iridoprocne bicolor* (Vieillot). Tree Swallow**

Arrived at Atlin on June 3. Found by us nesting only about human habitations, but during the third week in July there were so many young tree swallows gathered upon the largest of the three islands nearest to Atlin that it seemed as though they must have been reared elsewhere than in the town.

***Tachycineta thalassina lepida* Mearns**

**Northern Violet-green Swallow**

Abundant at Skagway, May 21, at Carcross, May 22, and at Atlin, when we reached there on May 28. Last seen near Atlin on September 1. There are no rocky ledges near Atlin, such as the violet-green swallow occupies elsewhere in the north, and as with all the other swallows found breeding in the region, they were nesting about human habitations, occupied or deserted, and nowhere else.

***Riparia riparia* (Linnaeus). Bank Swallow**

A flock of migrating bank swallows appeared near Atlin on June 10, and a single bird was seen on July 12. The species was not otherwise observed.

***Bombycilla garrula pallidiceps* Reichenow. Bohemian Waxwing**

A single bird seen at Carcross, May 24. At Atlin, the third week in May, waxwings were fairly common and in pairs. On June 3 the beginning of a nest was found, on June 4 one that was ready for lining, and on June 11 the first set of eggs. These and several other nests were on the mainland, not far from the lake shore, and in rather open groves of jack pine. Nests were mostly near the ground, the highest being some thirty feet up. They were all in the terminal forks of downward drooping branches, six to ten feet from the trunk.

Waxwings build their nests in scattered communities, so that where one pair is found there are pretty sure to be others not far distant. Within a few miles of Atlin there were several such groups, comprising at least eight or ten pairs at each place. We collected but three sets of eggs at these places, but evidently there was some more formidable enemy of the birds at work, for the waxwings gradually disappeared, and not one young bird was reared in these colonies.

On July 15 we made the first of several visits to three small islands opposite Atlin, and there we found waxwings in numbers, and nesting. Apparently every pair that had started the breeding season on the nearby mainland had moved out to the islands, where they seemed free of whatever scourge it was that had destroyed their first nests. We saw no Canada jays, no squirrels, and no chipmunks on the islands; any or all of these may have been responsible for the shifting of the birds.

On the mainland nests were all in jack pines, but on the islands they were nearly all in small balsam firs. Mostly they were built low, ten feet from the ground or less, and several were within reach from the ground. During the third week in July nests held fresh eggs or incomplete sets. Complete sets, on the islands and on the mainland, ranged from four to six eggs.

On Otter Creek, July 26 to August 9, waxwings were occasionally encountered, in small flocks, old and young together. During August the species almost entirely disappeared, days and weeks passing without one being seen. On September 7 a small flock was seen near Gladys Lake, and on the 10th another flock between Gladys Lake and Lake Teslin. Not seen subsequently, though the species might be expected to remain until a much later date.

Three waxwings were collected (nos. 44894-44896), male and female taken July 27, full grown but in juvenal plumage throughout, and an adult male, August 5, not yet beginning the annual molt. The young male has four large wax tips on each wing, the young female, two small ones. Neither has the vivid orange tail tipping noted on certain young birds from the Stikine River (Swarth, 1922, p. 279), though the female shows an approach to that color.

### ***Lanius borealis* Vieillot. Northern Shrike**

Our discovery of the northern shrike in the Atlin region establishes this bird as a breeding species in extreme northern British Columbia, though the previous capture of one by W. H. Osgood, for the U. S.

Biological Survey, at Bennett, June 9, 1903, made it a fair presumption that this was the case. We found no nest, but on June 30 we collected a brood of six young, just able to fly; the nest must have been close by. The young birds, huddled together in a spruce thicket, were being fed by one parent, which escaped. This was at the head of Cañon Creek, altitude 4000 feet, in a sparsely wooded mountain valley, close to the upper limit of upright timber. The young birds were extremely noisy; it was the incessant squalling for food that drew our attention, from a distance. Their stomachs were well filled, mostly with insect remains, including some small *Coleoptera*; in one stomach there were parts of a very young ptarmigan chick, including the bill. Three of the young were preserved by Brooks, three by Swarth (nos. 44897-44899).

On July 28 an adult male (no. 44900) was collected at the head of Otter Creek (about 3500 feet altitude). This bird is in the midst of the annual molt. Above and below the old feathers are extremely pale colored. The underparts are almost pure white, the old feathers having lost every vestige of the dusky vermiculations. Such markings show plainly enough on the new breast feathers, just coming in. The stomach held insect remains. The species was observed only on these two occasions.

A notable feature of the shrikes in juvenal plumage is their gray coloration. In the freshly acquired first winter plumage there is a decidedly brown tone both above and below, but, save for the wing markings, none of this appears in the juvenal stage. This plumage is mostly clear gray, slightly darker on the dorsum, and finely vermiculated below.

Through the courtesy of Dr. Louis B. Bishop there are available from his collection 57 specimens of *Lanius borealis*, about equally divided between eastern and western localities. In this museum there are twenty-six skins, fourteen western and twelve eastern. From the Carnegie Museum, Pittsburgh, I was able to borrow two adult males from the east side of Hudson Bay. These two, with one from Magdalen Island, in the Bishop collection, are the only breeding birds I have seen from eastern localities.

The subspecies *invictus* (Grinnell, 1900, p. 54), described from the Kowak River, Alaska, was characterized as of larger size, paler coloration dorsally, and with the white markings greater in extent, as compared with eastern birds. I can distinguish a slight average difference in size (see table), and, in some specimens, in the color characters also.

Certain Alaskan skins are paler colored than any eastern birds, and some have decidedly more extensive white markings (as on the lateral rectrices) than most eastern skins. An exceptional British Columbian specimen has the outer rectrices entirely white. There are Alaskan birds, though, that lie well within the range of variation of eastern birds, and there are one or two eastern birds with white markings on the tail feathers nearly as extensive as in any western ones.

There are a number of winter birds in this series from points lying between the Great Lakes and the Rocky Mountains, and nearly all of these I am unable to allocate to an eastern or a western race with any degree of assurance. Thus, while recognizing in the northern shrike a tendency toward development of the characters ascribed to *invictus* in the western part of its habitat, it seems to me so impossible to define the boundary between an eastern and a western race, or to identify most winter birds taken south of the breeding range, that I am disinclined to use different names for the variations exhibited.

***Vireosylva gilva swainsonii* (Baird). Western Warbling Vireo**

A rare species, here probably at the extreme northern limit of its range. First seen June 8, and from then on, at this one place, a vireo could be seen or heard singing at almost any time during the next few weeks. The indications were that a pair was nesting thereabout. The only other occasion on which the species was seen was on August 17, when one bird was collected by Brooks.

***Vermivora celata celata* (Say). Orange-crowned Warbler**

Migrating, not uncommonly, about Atlin, during August. Three specimens were collected (nos. 44901-44903), two females taken August 13, and one male on August 17, all immatures in first winter plumage. Others of this subspecies, easily recognized as a rule by the gray head, were seen until August 31.

***Vermivora celata orestera* Oberholser**

**Rocky Mountain Orange-crowned Warbler**

An "orange-crowned warbler," apparently of this subspecies, was seen at Carcross, May 24. Small numbers were migrating through the Atlin region during the last week in May and first week in June, and a few pairs bred in the lowlands thereabout, where they were seen

MEASUREMENTS IN MILLIMETERS (AVERAGE, MINIMUM AND MAXIMUM) OF *LANIUS BOREALIS*

|   | Wing                | Tail                | Culmen           | Tarsus           | White spot on outer tail feather |
|---|---------------------|---------------------|------------------|------------------|----------------------------------|
| 7 adult males from Alaska and British Columbia    | 117 0 (113 0-119 0) | 111 7 (107 0-116 5) | 17 6 (16 5-18 5) | 26 6 (25 5-27 2) | 46 1 (41 0-54 0)                 |
| 7 immature males from Alaska and British Columbia | 115 6 (114 0-116 5) | 109 4 (106 5-111 5) | 17 6 (17 0-18 0) | 26 9 (26 2-28 0) | 48 5 (35 0-91 0*)                |
| 10 adult males from eastern North America†        | 112 7 (111 0-115 0) | 107 9 (104 0-111 0) | 17 6 (17 0-18 2) | 26 5 (25 0-27 0) | 39 5 (31 0-55 0)                 |

\* Entire feather is white

† New York, 1, Rhode Island, 1 Connecticut, 5 Ontario 3

this molt was finished, but the adults apparently left as soon as the young could care for themselves. No old bird was seen after August 1, and the last few that were noted were still in breeding plumage. The black-poll warbler was numerous up to August 22; the last was seen on August 27.

The Atlin region may be assumed to be about the southwestern limit of the breeding range of this species, and in view of the abundance of the birds at that point it is of interest to note their scarcity farther south in British Columbia. There are only a few scattered records, all but one during fall migration, the southernmost at Quesnelle. Apparently the black-poll warbler has an east and west route over the Rocky Mountains of northern British Columbia, seldom or never traversing the southern two-thirds of the province.

Eleven specimens were collected (nos. 44935-44945), one adult female, four in juvenal plumage, four in various stages of the post-juvenal molt, and two in first winter plumage.

***Dendroica townsendi* (J. K. Townsend). Townsend Warbler**

A few pairs were nesting at isolated points in the lowlands, in clumps of tall spruce trees. They remained in the tree tops and would have been overlooked entirely during the breeding season were it not for the singing males. During the second week in August, young birds in completely acquired first winter plumage appeared in the poplar woods, and, while they were never numerous, some were seen daily thereafter during that month. Last noted August 31.

Two specimens were collected, an adult male, June 5 (no. 44946), an immature male, August 14 (no. 44947).

***Seiurus noveboracensis notabilis* Ridgway. Grinnell Water-thrush**

One was collected by Brooks in the bottom lands of Pine Creek near Atlin, August 21. This was the only one seen.

***Geothlypis trichas occidentalis* Brewster. Western Yellowthroat**

On September 10 I saw several and heard others in the marsh at Fat Creek, six or seven miles southwest from Lake Teslin and just north of the British Columbia-Yukon boundary. On September 13, returning over the same trail, no yellowthroats were seen. Not otherwise observed in the Atlin region, to my surprise, for in September,

1909, I had found the species on the lower Taku River, Alaska, which drains from the country immediately south of Lake Atlin (see Swarth, 1911, p. 101). Occurrence in migration on the lower reaches of the stream would imply occurrence also toward the head of the river.

***Wilsonia pusilla pileolata* (Pallas). Pileolated Warbler**

Seen at Carcross on May 22 and subsequently, and, in small numbers, migrating in the Atlin lowlands during the first week in June. Occasional birds were seen near Atlin throughout the summer, and these may have been nesting there, but the breeding ground for the most part, if not entirely, lies above timber line. On the higher ridges, pileolated warblers could always be found in the balsam thickets, where, presumably, the nests were placed.

On August 8, migrating pileolated warblers, with some other small birds, were flitting through the bushes on the summit of Spruce Mountain. Throughout August they could be found daily in small numbers in the poplar woods around Atlin. The last one seen was at Lake Teslin, September 12.

Three specimens were collected (nos. 44948–44950), an adult male and two immature males.

***Setophaga ruticilla* (Linnaeus). American Redstart**

One bird was collected near Atlin by Brooks on June 14, another (no. 44951) by myself on June 17, and several others were seen during June and July. Atlin must be at practically the northwestern limit of distribution of this species.

***Anthus rubescens* (Tunstall). Pipit**

This species must breed in some parts of the mountains near Atlin, but we saw none until late in the summer. First encountered August 1, on the summit of Spruce Mountain, and seen several times during the next few days. These were mostly birds in juvenal plumage, but strong on the wing. First seen in the lowlands near Atlin on August 26, and frequently observed during the next few weeks. A small flock of pipits was seen from the steamer on Tagish Lake, as I was leaving, September 23.

Two specimens were collected (nos. 44952–44953), both in juvenal plumage, taken on the summit of Spruce Mountain, August 3.



**Sitta canadensis** Linnaeus. Red-breasted Nuthatch

A red-breasted nuthatch heard calling in woods near Atlin on June 5 was the only one of the species noted during the nesting season. Next seen (a single bird) on Spruce Mountain, August 1. During the latter part of August the species was migrating through the woods near Atlin in fair abundance. Last seen by me on August 31, though it may be expected to occur in this region until a much later date.

**Penthestes atricapillus septentrionalis** (Harris)

## Long-tailed Chickadee

Presumably resident in the region throughout the year, though not abundant. Seen at Carcross during the last week of May, and about Atlin during the whole of my stay, usually in poplar woods. Six specimens were collected (August 16 to 28), all in fresh fall plumage (nos. 44954-44959).

**Penthestes gambeli abbreviatus** Grinnell

## Short-tailed Mountain Chickadee

A male bird (no. 44960) in breeding condition was shot in spruce woods near Atlin, June 12. Presumably the species nests in this general region, but it was not otherwise observed. This is the northernmost station at which it has been found, Grand Rapids, on the Stikine River, 160 miles to the southward, being the nearest point of record (Swarth, 1922, p. 297).

**Penthestes hudsonicus columbianus** (Rhoads). Columbian Chickadee

A fairly common species in the Atlin region, more so than the long-tailed chickadee. Showed decided preference for spruce woods. Twenty-three specimens were collected (nos. 44961-44983), comprising six breeding adults, six juvenals, and three adults and eight immatures in fresh fall plumage.

The subspecies *columbianus*, described by Rhoads (1893, p. 23), was included in the 1895 edition of the A. O. U. Check-list, but it was eliminated later (A. O. U. Committee, 1908, p. 355) for reasons that are not known to me. The series of birds above listed, together with others from more southern points in British Columbia (see Swarth,

1924, p. 368) strongly support the validity of the race. Compared with series of specimens from more northern points in Alaska, assumed to be typical *hudsonicus*, they exhibit, conclusively as it seems to me, the color characters ascribed to *columbianus* by Rhoads (*loc. cit.*) and by Ridgway (1904, p. 414).

***Regulus satrapa olivaceus* Baird.** Western Golden-crowned Kinglet

Seen but once, a single bird near Atlin on May 29.

***Regulus calendula calendula* (Linnaeus).** Ruby-crowned Kinglet

Seen at Carcross on May 24. Found in small numbers throughout the lowlands of the Atlin region during the summer and in rather greater abundance after the southward migration began. The first broods of young appeared on July 16. Seen daily during the early part of September, and one bird was seen at Carcross on September 24. Four specimens were collected (nos. 44984-44987).

***Myadestes townsendi* (Audubon).** Townsend Solitaire

Breeds in small numbers about Atlin, mostly on the partly open mountain sides just below timber line. First seen on May 29, the last September 1. (One specimen collected, a juvenal male, June 30 (no. 44988).

***Hylocichla ustulata swainsoni* (Tschudi).** Olive-backed Thrush

Breeds in fair abundance in the poplar and willow woods of the lowlands. Arrived June 4; last seen August 29. Nine specimens were collected (nos. 44989-44997). These, together with others from previous expeditions to the Stikine and Skeena valleys, comprise a series of forty-one specimens of olive-backed thrush from northern British Columbia now in this museum. This series throughout exhibits the grayish dorsal coloration described by Oberholser (1898, p. 304) as the principal character of *Hylocichla ustulata almae*. I would be inclined to recognize that subspecies were it not for the fact that the same coloration occurs in series from eastern localities, among the more numerous olivaceous-backed birds that are supposed to represent typical *swainsoni*. The name *almae* may well rest in abeyance for the time being until a better understanding is reached of the meaning

of these color variations. However, while these gray-backed birds do occur throughout the east, the extreme olivaceous type of coloration seen commonly in eastern birds is not found in series of breeding birds from the northwest, in British Columbia and Alaska (see Bishop, 1900, p. 119).

***Hylocichla guttata guttata* (Pallas).** Alaska Hermit Thrush

A fairly common species in the lowlands. Seen at Carcross, May 22, and at Atlin upon our arrival there, May 28. The last bird was seen September 19.

Three nests were found: One, June 13, with three fresh eggs; one June 23, with four fresh eggs; and one July 12, with four fresh eggs. All were on the ground, the first in a clump of small willows at the edge of a muskeg, the second in an opening in mixed poplar and spruce woods, and the third in rather dense poplar woods. It seems noteworthy that this species should be nesting upon the ground here, in view of the fact that on the upper Stikine River, a short distance to the southward, hermit thrush nests were found placed in small spruce trees several feet from the ground (Swarth, 1922, p. 303).

Ten specimens were collected, two breeding adults, one juvenal, three in the post-juvenal molt, and four immatures in fresh fall plumage (nos. 44998-45001, 45003-45008). One or two of the fall birds show slight intergradation toward *pallasii*, in the buffier, less grayish flanks, and in dorsal coloration.

***Hylocichla guttata pallasii* (Cabanis).** Eastern Hermit Thrush

One specimen collected, an immature female on migration, August 23 (no. 45002). This bird is essentially like two others collected by myself in the Skeena Valley (Swarth, 1924, p. 370), and, like those birds, while not as bright reddish as typical *pallasii*, it is distinctly nearer to that form than to the darker, gray-flanked *guttata*, the breeding bird of northern British Columbia.

***Planesticus migratorius migratorius* (Linnaeus).** Eastern Robin

Present at Carcross, May 22, and at Atlin upon our arrival there a few days later. Last seen August 31. Robins breed in fair abundance in the more open woods in the valleys. They shun the dense spruce woods of the middle altitudes, but are present again in some numbers at timber line, where the scattered balsam thickets supply needed shelter. Many old nests were found in these trees.

The first young out of the nest was seen June 11. During August robins were gathered in noisy flocks, twenty or thirty together, preparatory to departure for the south.

Four specimens were collected (nos. 45009-45012), one adult male, two in juvenal plumage, and one adult female taken August 16, which had then finished the annual molt.

***Ixoreus naevius meruloides*** (Swainson). Northern Varied Thrush

The varied thrush apparently does not breed in the Atlin region, for it was encountered nowhere during the summer months. First appeared on September 5, when several were seen, evidently migrating southward. A few others were noted, near Atlin and at points between Atlin and Teslin, the last on September 21. One specimen was collected, a female taken September 5 (no. 45013); it is typical of the subspecies *meruloides*.

***Sialia currucoides*** (Bechstein). Mountain Bluebird

A fairly common species and with a predilection for human habitations, whether occupied or abandoned. Seen at Carcross, May 22, and at Atlin when we arrived. Young birds were flying about during the second week in July. The bluebirds linger to a later date than most of the summer visitants. I saw a flock of fifteen at Carcross on September 24.

CHECK LIST OF THE MAMMALS

1. *Sorex personatus personatus* I. Geoffroy
2. *Sorex obscurus obscurus* Merriam
3. *Neosorex navigator navigator* Baird
4. *Mustela cicognanii richardsonii* Bonaparte
5. *Gulo luscus* (Linnaeus)
6. *Vulpes alascensis abietorum* Merriam
7. *Canis lestes* Merriam
8. *Marmota caligata caligata* (Eschscholtz)
9. *Citellus plesius plesius* (Osgood)
10. *Eutamias minimus caniceps* Osgood
11. *Sciurus hudsonicus hudsonicus* (Erxleben)
12. *Castor canadensis canadensis* Kuhl
13. *Peromyscus maniculatus borealis* Mearns
14. *Neotoma cinerea saxamans* Osgood
15. *Synaptomys borealis dalli* Merriam
16. *Microtus drummondii* (Audubon and Bachman)
17. *Microtus mordax mordax* (Merriam)
18. *Ondatra zibethica spatulata* (Osgood)
19. *Erethizon epixanthum nigrescens* Allen
20. *Lepus americanus macfarlandi* Merriam
21. *Alces gigas* Miller

## GENERAL ACCOUNTS OF THE MAMMALS

The collection of mammals was inadequate and disappointing. I had not as much time to give to this work as would have been desirable, but, nevertheless, assiduous trapping in a variety of surroundings was so uniformly unsuccessful that failure could hardly have been due to any cause other than the actual scarcity of most of the smaller mammals. As an instance in point, trapping was carried on for a week at a place where lemmings were known to have been abundant at the same season in previous years, but not one was caught. At several places extensive systems of runways were trapped over for days and weeks with but an occasional mouse as a result. Another year might find small rodents swarming over the same region.

It was a question just what might be included in the following list; as it stands it comprises the species that were personally encountered and specifically identified. Bats were seen on several occasions but not collected. Atlin is in the center of a region that supports a large amount of big game (sheep, caribou, mountain goat, and bear) of species that I either did not encounter at all or so casually as not to be worth reporting. Similarly, there are fur bearers throughout the region regarding which I learned nothing. I saw skins of flying squirrels killed near Atlin, and there are doubtless yet other species still to be included in any comprehensive account of the mammals of this section.

***Sorex personatus personatus*** I. Geoffroy. Masked Shrew

Five specimens collected (nos. 34389-34393), one from Surprise Lake (3200 feet altitude), three from the head of Otter Creek (4000 feet altitude), and one from Atlin.

***Sorex obscurus obscurus*** Merriam. Dusky Shrew

Two specimens collected (nos. 34394-34395), from near the summit of Spruce Mountain (4500 feet altitude), on August 1.

***Neosorex navigator navigator*** Baird. Water Shrew

A water shrew, presumably of this form, was seen at the head of Otter Creek (4000 feet altitude), July 30. It was at mid-day, and the little animal was ascending a small stream, sometimes swimming in the pools, then running through the shallows. It dived when it saw me and did not appear again.

***Mustela cicognanii richardsonii* Bonaparte. Richardson Weasel**

Encountered but once during the summer, on July 14, when one was seen. It was enduring the attack of a number of Gambel sparrows that were protesting at the weasel's being abroad during the day.

***Gulo luscus* (Linnaeus). Wolverine**

I obtained from a trapper at Carcross the skull of a female wolverene (no. 34396) trapped by him some sixty miles west of Carcross, during the winter of 1923-24.

***Vulpes alascensis abietorum* Merriam. British Columbia Red Fox**

The collection includes a red fox skull, picked up on the summit of Spruce Mountain. The species was not otherwise encountered in a wild state. "Silver fox" farming is an established industry in this section, and both at Carcross and at Atlin there are successful fox farms.

***Canis lestes* Merriam. Northern Coyote**

The northern extension of the range of the coyote into this region seems to have taken place in relatively recent years, according to local report, but however that may be the species now occurs in some numbers at least as far north as southern Yukon Territory.

On August 3, five coyotes, apparently a family, were encountered on the summit of Spruce Mountain, above timber line (at about 5000 feet altitude), and two half-grown young ones (nos. 34397-34398) were shot. After my return to Berkeley I received skin and skull of an adult male coyote (no. 34992) trapped at Grouse Creek, Yukon Territory (just north of the British Columbia boundary, on the trail to Teslin), January 10, 1925, and of an adult female (no. 36469) trapped at Teslin, January 15, 1926.

In a letter received from Mr. A. B. Taylor, government telegraph operator at Atlin, and an accurate observer of animal life, under date of November 5, 1925, he states: "The country is overrun with coyotes, and they have pretty well cleaned out the rabbits and grouse. They come quite close to town and set up a howling that starts all the dogs, especially in the early morning, just before dawn. After the lake freezes there will be some sport chasing them in automobiles. One man got eight last winter in that way."

***Marmota caligata caligata* (Eschscholtz). Hoary Marmot**

A few were seen on various mountains not far from Atlin. The species is apparently of general distribution, though not numerous, above timber line (about 3500 feet) throughout the region. One specimen (no. 34276), an adult male, was collected by Brooks near Log Cabin (White Pass), on September 1.

***Citellus plesius plesius* (Osgood). Bennett Ground Squirrel**

Extremely abundant about Carcross. The grounds of the "Gopher Golf Club," on the outskirts of the town, supported a large population of the squirrels, as is suggested by the club's name, and we saw them elsewhere wherever we walked. The light sandy soil and open woods seem to form a favorable set of conditions for the species.

In the immediate vicinity of Atlin I saw no ground squirrels, but there were small colonies at certain points in the lowlands within a few miles of town. Above timber line on the nearby mountains they were present everywhere, in some places in great numbers. Along Otter Creek, ground squirrels fairly swarmed, the whole length of the valley and on the surrounding mountains. Between Surprise Lake and Teslin I saw none. Just what the important factors are that determine the local distribution of the species in this region could not be ascertained with certainty, but in general the ground squirrels favored open country.

The small colonies near Atlin were in open woods, and there were miles of similar woods where none was seen. Along Otter Creek they were numerous over ground that was densely grown with willow thickets. None was seen at any time, however, in even fairly dense woods of large conifers.

On August 24 ground squirrels were abundant and active on the summit of Monarch Mountain. On September 5, at the same place, none was seen. As this was a cold, stormy day, however, their disappearance may have been but temporary and due to the weather at that time.

Five specimens were preserved (nos. 34399-34403), one from Carcross, May 22, two from Spruce Mountain, July 31 and August 3, respectively, and two from Monarch Mountain, August 24.

**Eutamias minimus caniceps** Osgood. Gray-headed Chipmunk

Nine specimens collected (nos. 34410-34418), all adult. Chipmunks were seen about Carcross, and they were fairly common in the lowlands of the Atlin region. In the town they came familiarly about barns and in the gardens.

**Sciurus hudsonicus hudsonicus** (Erxleben)

## Northern Red Squirrel

Six specimens collected (nos. 34404-34409), all adults that are entirely or mostly in summer pelage. In this small series there is rather notable variation from grayish to reddish extremes; the reddish specimens may be taken to illustrate intergradation by individual variation toward *S. h. petulans* of the nearby Alaskan coast.

Red squirrels are fairly common and of general distribution throughout the wooded parts of the region.

**Castor canadensis canadensis** Kuhl. Beaver

Beaver have little chance of survival anywhere near human habitations unless accorded rigid protection, and throughout such parts of the Atlin region as we visited trapping had reduced their numbers to the vanishing point. On the evening of September 9 I spent an hour or more watching a pair of beavers in a pond a few miles north of the British Columbia-Yukon boundary, on the trail to Lake Teslin. They were then actively engaged in laying away winter stores, in the shape of willow cuttings, and trip after trip, with monotonous regularity, was made by the laboring animals, across the pond to the growing willows, and back to the house again, where entrance was effected by diving.

**Peromyscus maniculatus borealis** Mearns

## Northern White-footed Mouse

Thirteen specimens were collected (nos. 34419-34431), twelve from the vicinity of Atlin, and one from lower Otter Creek. White-footed mice were about as scarce as the other small rodents of the region, and even this small series was acquired, usually one specimen at a time, at long intervals through the summer.



**Neotoma cinerea saxamans** Osgood. Northern Bushy-tailed Wood Rat

Three specimens collected (nos. 34432–34434), one at Atlin and two at our camp on lower Otter Creek. In this region, as elsewhere in the northwest, the wood rat is more or less of a pest, invading cabins and destroying or carrying away almost anything that can be moved. We saw slight trace of the presence of this species, however, and it seems likely that the wood rats had suffered temporary reduction of numbers together with other small rodents.

**Synaptomys borealis dalli** Merriam. Dall Lemming Mouse

One specimen (no. 34435), a young male, was trapped on upper Otter Creek (3800 feet altitude), on July 30. The species was not otherwise encountered.

**Microtus drummondii** (Audubon and Bachman)

## Drummond Meadow Mouse

Fourteen specimens were preserved (nos. 34436–34449), thirteen from the vicinity of Atlin and one from the summit of Spruce Mountain (5000 feet altitude). They were rare, one specimen in two or three nights being the most to be hoped for in a line of twenty-five or thirty traps.

**Microtus mordax mordax** (Merriam). Cantankerous Meadow Mouse

Nine specimens were collected (nos. 34450–34458), four from Atlin, four from Otter Creek (3000 to 4000 feet altitude), and one from near the summit of Spruce Mountain (5000 feet altitude). These nine specimens represent approximately the result of eighty traps set out for two weeks. Not that just that number of traps was set for exactly that number of days at any one period, but that would be about the sum total from traps placed where *Microtus* should have been trapped. Two pregnant females contained three and four embryos, respectively. In an extensive series from the upper Stikine River, trapped when the animals were abundant, the number of embryos was usually five or six.

**Ondatra zibethica spatulata** (Osgood). Northwestern Muskrat

Muskrats were seen at various times in ponds at the edge of the town of Atlin, and elsewhere in suitable places east to Lake Teslin. The species is abundant throughout this whole region.

**Erethizon epixanthum nigrescens** Allen. Dusky Porcupine

A porcupine killed while it was invading the garden at the mounted police post at Nisuttlin Bay, Teslin Lake, on September 11, was the only one seen all summer.

**Lepus americanus macfarlani** Merriam. Mackenzie Varying Hare

Abundant everywhere in the lowlands. In crossing White Pass, May 21, we saw rabbits from the train when we had descended on the east slope as far as the upper edge of timber. At Carcross they were seen daily during our short stay, as they were also in the woods near Atlin throughout the summer. Stands of young poplars and sometimes of young jack-pine were attacked and girdled by the rabbits on such a scale that over areas acres in extent well nigh every tree would be killed. Larger trees, too, were sufferers to some extent (see pl. 8). Where trees had been chopped down and the smaller branches left piled to one side, these brush piles were invariably browsed upon by rabbits until nearly every vestige of bark was removed.

Five specimens were collected (nos. 34459-34463). An adult male shot July 10 still has white feet and white margined ears. In an adult female taken August 22 the feet are buffy and there is no white on the ears. An adult male shot September 21 has both front and hind legs white and the ears are mostly white.

These animals, all in summer pelage, are notably more grayish colored, less reddish, than varying hares from the upper Skeena Valley, which I have elsewhere (Swarth, 1924, p. 384) referred to the subspecies *L. a. columbiensis*.

**Alces gigas** Miller. Alaska Moose

Abundant throughout the region. Fresh tracks were seen constantly within a few miles of the town of Atlin, both in the lowlands and well up on the mountain slopes. On the shores of Lake Teslin I saw certain favored spots where the muddy banks were trodden like cattle yards. That but few of the animals were seen by us through the summer was largely due, of course, to the fact that, not hunting for them, we made no effort to avoid noises and actions that would alarm them; nevertheless, they showed wariness and ability in keeping out of sight. In a country similarly populated with deer many more of those animals would have been encountered.

## LITERATURE CITED

## AMERICAN ORNITHOLOGISTS' UNION COMMITTEE

1908. Fourteenth supplement to the American Ornithologists' Union check-list of North American birds. *Auk*, 25, 343-399.  
1910. Check-list of North American birds (ed. 3, revised; New York, American Ornithologists' Union), 430 pp., 2 maps.

## ANDERSON, E. M.

1915. Birds collected and observed in the Atlin district, 1914. Report of the Provincial Museum of Natural History for the year 1914 (Victoria, British Columbia), pp. 8-17.

## AUDUBON, J. J.

1830. The birds of America (London, published by the author), 1, pls. 1-100.

## BAILEY, B. H.

1916. Krider's hawk (*Buteo borealis krideri*) in Alaska. *Auk*, 33, 321.

## BAIRD, S. F. ("with the coöperation of" CASSIN, J., AND LAWRENCE, G. N.)

1858. Birds. Pacific Railroad Reports, 9, lvi + 1005 pp.

## BAIRD, S. F., BREWER, T. M., AND RIDGWAY, R.

1874. A history of North American birds. Land birds (Little, Brown and Co., Boston), 3, 560 + xxviii pp., pls. 57-64, many figs in text.

## BENT, A. C.

1921. Life histories of North American gulls and terns, order *Longipennes*. U. S. Nat. Mus. Bull., 113, x + 345 pp., 93 pls.

## BEYER, G. E., ALLISON, A., AND KOPMAN, H. H.

1908. List of the birds of Louisiana. Part v. *Auk*, 25, 439-448.

## BISHOP, L. B.

- 1900a. Birds of the Yukon region, with notes on other species. U. S. Dept. Agr., Biol. Surv., N. Am. Fauna, 19, 47-96.  
1900b. Descriptions of three new birds from Alaska. *Auk*, 17, 113-120.

## BREWER, T. M.

1878. Nest and eggs of *Zonotrichia coronata*. Bull. Nuttall Ornith. Club, 3, 42-43.

## BREWSTER, W.

1890. A new subspecies of the solitary sandpiper. *Auk*, 7, 377-379.

## BROOKS, A.

1912. Some British Columbia records. *Auk*, 29, 252-253.  
1926. The display of Richardson's grouse, with some notes on the species and subspecies of the genus *Dendragapus*. *Auk*, 43, 281-287, pls. 10-11.

CLARK, A. H.

1910. The birds collected and observed during the cruise of the United States Fisheries Steamer "Albatross" in the North Pacific Ocean, and in Bering, Okhotsk, Japan, and eastern seas, from April to December, 1906. *Proc. U. S. Nat. Mus.*, **38**, 25-74.

COUES, E.

1880. "Behind the veil." *Bull. Nuttall Ornith. Club*, **5**, 193-204.

DICKEY, D. R., AND VAN ROSSEM, A. J.

1923. Description of a new grouse from southern California. *Condor*, **25**, 168-169.

DWIGHT, J., JR.

1900. The moult of the North American *Tetraonidae* (quails, partridges and grouse). *Auk*, **17**, 34-51, 143-166, pls. 4-5.

GMELIN, J. F., ED.

- 1788-1789. Linné. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (cura Jo. Frid. Gmelin, Lipsiae, Beer), **1**, [x] + 1032 pp.

GRINNELL, J.

1900. Birds of the Kotzebue Sound region, Alaska. *Pacific Coast Avifauna*, **1**, 80 pp., 1 pl. (map).  
1910. Birds of the 1908 Alexander Alaska expedition, with a note on the avifaunal relationships of the Prince William Sound district. *Univ. Calif. Publ. Zool.*, **5**, 361-428, pls. 33-34, 9 figs. in text.

HARTERT, E.

1921. Die vögel der paläarktischen fauna (Berlin), **3**, 1765-1892.

HEERMANN, A. L.

1859. Report upon the birds collected on the survey. *Pacific Railroad Reports*, **10**, part 4, pp. 29-80, 7 pls.

HOFFMANN, R.

1924. Notes on the flight performance of the Wilson snipe. *Condor*, **26**, 175-176.

KERMODE, F., AND ANDERSON, E. M.

1914. Report on birds collected and observed during September, 1913, on Atlin Lake, from Atlin to south end of the lake. Report of the Provincial Museum of Natural History for the year 1913 (Victoria, British Columbia), pp. 19-21.

OBERHOLSER, H. C.

1898. Description of a new North American thrush. *Auk*, **15**, 303-306.  
1905. The forms of *Vermivora celata* (Say). *Auk*, **22**, 242-247.

OSGOOD, W. H.

1900. Results of a biological reconnoissance of the Yukon River region. General account of the region. *U. S. Dept. Agr., Biol. Surv., N. Am. Fauna*, **19**, 7-20, pls. 2-3.  
1904. A biological reconnoissance of the base of the Alaska Peninsula. *U. S. Dept. Agr., Biol. Surv., N. Am. Fauna*, **28**, 285 pp., 8 pls.

RHOADS, S. N.

1893. Notes on certain Washington and British Columbia birds. *Auk*, 10, 16-24.

RIDGWAY, R.

1904. The birds of North and Middle America. U. S. Nat. Mus. Bull., 50, Part III, xx + 801 pp., 19 pls.  
 1912. Color standards and color nomenclature (Washington, D. C.; published by the author), 3 + 44 pp., 53 pls.  
 1919. The birds of North and Middle America. U. S. Nat. Mus. Bull., 50, Part VIII, xvi + 852 pp., 33 pls.

RILEY, J. H.

1911. Descriptions of three new birds from Canada. *Proc. Biol. Soc. Wash.*, 24, 233-236.  
 1912. Birds collected or observed on the expedition of the Alpine Club of Canada to Jasper Park, Yellowhead Pass, and Mount Robson region. *Canadian Alpine Journal*, special number, pp. 47-75, pls. 1-2.

SHARPE, R. B.

1874. Catalogue of the Accipitres, or diurnal birds of prey, in the collection of the British Museum. *Catalogue of Birds*, 1, xiii + 480 pp., 14 pls., many text figs.

STEJNEGER, L.

1885. Results of ornithological explorations in the Commander Islands and in Kamtschatka. U. S. Nat. Mus. Bull., 29, 382 pp., 8 pls., several text figs.

SWARTH, H. S.

1911. Birds and mammals of the 1909 Alexander Alaska expedition. *Univ. Calif. Publ. Zool.*, 7, 9-172, pls. 1-6.  
 1920. Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. *Univ. Calif. Publ. Zool.*, 21, 75-224, pls. 4-7, 30 text figs.  
 1922. Birds and mammals of the Stikine River region of northern British Columbia and southeastern Alaska. *Univ. Calif. Publ. Zool.*, 24, 125-314, pl. 8, 34 text figs.  
 1924. Birds and mammals of the Skeena River region of northern British Columbia. *Univ. Calif. Publ. Zool.*, 24, 315-394, pls. 9-11, 1 text fig.

SWARTH, H. S., AND BROOKS, A.

1925. The timberline sparrow, a new species from northwestern Canada. *Condor*, 27, 67-69.

TAVERNER, P. A.

1914. A new subspecies of *Dendragapus* (*Dendragapus obscurus flemingi*) from southern Yukon Territory. *Auk*, 31, 385-388.

1916. Preliminary list of specimens taken by C. H. Young and William Spreadborough, at Brackendale, Lillooet, and McGillivray Creek, British Columbia, between June 11 and September 12, 1916. Summary Report, Geol. Surv., Dept. of Mines, Ottawa, pp. 359-368.
1918. Trinomials and current practice. *Condor*, 20, 213-216.

THAYER, J. E., AND BANGS, O.

1914. Notes on the birds and mammals of the Arctic coast of east Siberia. Birds. *Proc. New England Zool. Club*, 5, 3-48.

VAN ROSSEM, A. J.

1925. Flight feathers as age indicators in *Dendragapus*. *Ibis*, ser. 12, no. 2, pp. 417-422, text figs. 10-12.

## PLATE 5

**Fig. 2.** Islands in Lake Atlin opposite the town. These islands are clothed with balsam fir, which does not grow on the adjacent mainland at this level. They are much more densely populated with small land birds than is the mainland, and several species of water birds nest there also. Photo taken September 6, 1924.

**Fig. 3.** "Blue Cañon," at about 4000 feet elevation on upper Spruce Creek; a scene of former mining activities. The valley and lower mountain slopes here shown are typical of the habitat of the willow ptarmigan in this region. The rock and white-tailed ptarmigans inhabit the higher ridges. Photo taken September 1, 1924.



Fig 2



Fig 3



## PLATE 6

Fig. 4. Lake at the head of Cañon Creek, about 4000 feet altitude, near Atlin. Willow ptarmigan nested abundantly here, Fleming grouse were in the timber on the adjacent slopes, western tree sparrows were present in great numbers in the bushes about the lake, a brood of northern shrikes was found in the fir trees on the left, and families of eared grebes and Barrow golden-eyes were swimming about the lake. Photo taken July 18, 1924.

Fig. 5. North-facing slope of Monarch Mountain, near Atlin. The summit is at about 5000 feet altitude, the base, about 2500 feet. The recent snowfall, conspicuous on the timberless summit, indicates the upper limit of forest trees on the mountain. Photo taken September 22, 1924.

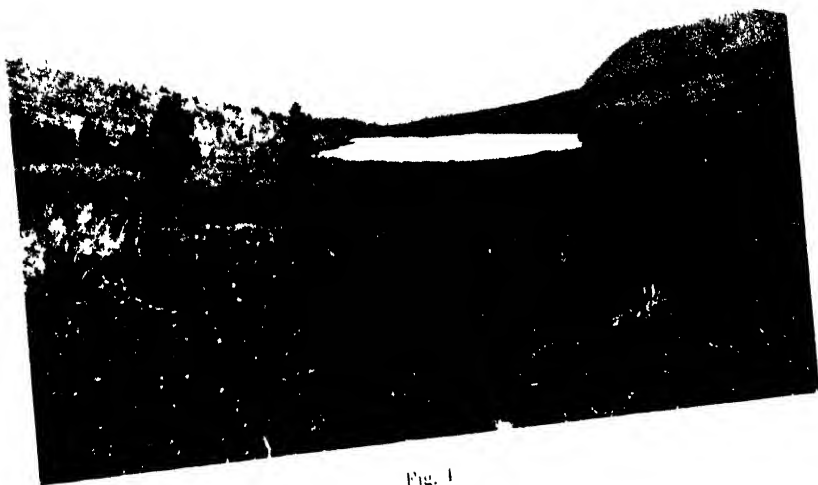


Fig. 4



Fig. 5

## PLATE 7

**Fig. 6.** Nest site of golden-crowned sparrow, on the summit of Monarch Mountain. The nest was on the ground in the brush (trailing birch) at the left of the thicket of balsam. The balsam trees shown are about ten feet high. Photo taken June 22, 1924.

**Fig. 7.** Nest of golden-crowned sparrow, on the ground, in grass, under a tangle of trailing birch. Photo taken June 22, 1924.



Fig. 6

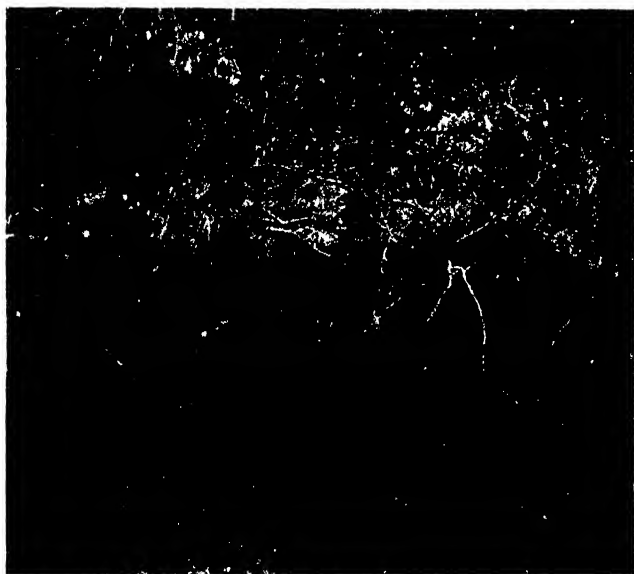


Fig. 7

## PLATE 8

“Poplars” (quaking aspen) girdled by rabbits, a common sight in the woods when these animals are abundant. The largest trees shown are four or five inches in diameter. The highest points gnawed by the animals, some three or four feet above the ground, were reached in winter when snow lay deep about the trees. Photo taken June 6, 1924.





NEW SUBSPECIES OF BIRDS (PENTHESTES,  
BAEOLOPHUS, PSALTRIPARUS, CHAMAEA)  
FROM THE PACIFIC COAST OF  
NORTH AMERICA

BY  
JOSEPH GRINNELL AND HARRY S. SWARTH



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 5, pp. 163-175, 2 figures in text  
Issued September 16, 1926

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# NEW SUBSPECIES OF BIRDS (PENTHESTES, BAEOLOPHUS, PSALTRIPARUS, CHAMAEA) FROM THE PACIFIC COAST OF NORTH AMERICA

BY

JOSEPH GRINNELL AND HARRY S. SWARTH

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

The following contribution to vertebrate systematics is based primarily upon recently received collections of birds from the San Pedro Martir region of Lower California. These collections have been gathered incidentally to a program of faunal exploration in that territory, which program was undertaken early last year at the suggestion of, and with means provided by, Miss Annie M. Alexander. The present paper is thus, in final analysis, a further result of Miss Alexander's deep interest in the development of a detailed knowledge of the animal life of western North America.

## ***Penthestes gambeli atratus*, new subspecies**

San Pedro Martir Mountain Chickadee

*Type*.—Male adult; no. 46490, Mus. Vert. Zool.; La Grulla, 7200 feet, Sierra San Pedro Martir, Lower California, Mexico; October 12, 1925; collected by J. Grinnell; original no. 6502.

*Distinguishing characters*.—Differs from *Penthestes gambeli baileyae* (Grinnell, 1908, p. 29), to which it is nearest geographically, in longer tail, in slightly darker general coloration, and most especially in restriction of the superciliary and frontal white.

*Range*.—So far as known, only the main plateau of the Sierra San Pedro Martir, whence 26 specimens are available from the neighborhoods of Concepcion, 6000 feet altitude, La Grulla, 7200 feet, and Vallecitos, 7500–8500 feet. Adheres closely to the coniferous belt of the Transition and Canadian life-zones.

*Measurements*.—In millimeters (average, minimum and maximum), of 6 males of *Penthestes gambeli atratus* from the Sierra San Pedro Martir: wing, 69.4 (65.0–71.5); tail, 61.2 (60.0–62.5); exposed culmen, 10.0 (9.2–11.0). Of 8 males of *P. g. baileyae* from San Diego and Los Angeles counties, California: wing, 67.4 (66.0–69.0); tail, 57.7 (56.0–59.5); exposed culmen, 9.9 (9.0–10.5).

*Remarks.*—The race of Mountain Chickadee of the Sierra San Pedro Martir, as compared with related subspecies, exhibits an appreciable darkening of the plumage in the direction not of brown but of slate. This darkening is most apparent on the flight feathers, which are slaty black as compared with the more brownish-hued quill feathers of other races; but it shows also in more leaden-hued flanks and upper parts. This general leaden tone of coloration is quite apparent in fresh plumaged birds, but it is a character that tends to be lost even when the feathers become only slightly worn.

Together with this darkening there is restriction in the area covered by the one conspicuous white marking on this bird, the superciliary stripe, which marking extends forward in fresh plumage to nearly or quite meet its fellow on the forehead. The white on the head of *atratus* is not only less in area occupied, but it is *shallower*; and birds in breeding plumage, when it is reduced or effaced by wear, come to bear a curious resemblance about the head to *Penthestes atricapillus*.

The generally dark hue of *atratus* might be regarded as simply a further development of one of the characters that distinguishes *baileyae* from more northern races if the Mountain Chickadee were the only species concerned; but from conditions found in many other of the birds of the same section of Lower California this character is seen to be one that is more or less strongly and similarly developed in several diverse species. Furthermore, the distinctly longer tail of *atratus* is a departure from *baileyae* in an unexpected direction, not in conformity with any apparent rule among the other associated species.

### ***Baeolophus inornatus affabilis*, new subspecies**

San Pedro Martir Plain Titmouse

*Type.*—Male; no. 47074, Mus. Vert. Zool.; Concepcion, 6000 feet altitude, Sierra San Pedro Martir, Lower California, Mexico; November 20, 1925; collected by Chester C. Lamb; original no. 5278.

*Distinguishing characters.*—As compared with *Baeolophus inornatus murinus* and *B. i. inornatus* occurring to the northward, of more plumbeous coloration; bill large, as in *murinus*. This is the darkest, most leaden colored, of any of the subspecies of *Baeolophus inornatus*, showing no trace of the brown tinge that is apparent strongly in *inornatus* and somewhat less so in *murinus*. The generally dark tone of *affabilis* extends even to bill and feet, which are definitely black. In the other subspecies those parts are usually brownish tinged.

MEASUREMENTS (AVERAGE, MINIMUM AND MAXIMUM) OF SUBSPECIES OF *BAEOLOPHUS INORNATUS*

|   | Wing             | Tail             | Culmen           | Tarsus           | Middle toe with claw |
|---|------------------|------------------|------------------|------------------|----------------------|
| <i>B. i. sequestratus</i><br>10 males, Jackson County, Oregon.                    | 67.8 (66.0-70.0) | 57.4 (56.0-58.5) | 10.1 (10.0-10.2) | 19.9 (19.0-20.5) | 16.7 (16.0-17.2)     |
| <i>B. i. nornatus</i><br>10 males, Monterey and Santa Clara counties, California. | 68.6 (65.0-71.0) | 59.2 (56.5-62.0) | 10.9 (10.0-11.5) | 21.1 (20.2-21.5) | 16.9 (16.0-17.5)     |
| <i>B. i. murinus</i><br>10 males, Los Angeles and San Diego counties, California. | 69.5 (67.0-72.0) | 59.8 (57.5-63.0) | 11.6 (11.0-12.0) | 20.8 (20.0-22.0) | 17.0                 |
| <i>B. i. affabilis</i><br>8 males, Sierra San Pedro Martir, Lower California.     | 71.9 (70.0-74.0) | 62.6 (59.2-65.0) | 11.8 (11.2-12.2) | 21.3 (21.0-21.5) | 16.9 (16.0-18.0)     |

*Range*.—Seemingly confined to a limited area on the west slope of the Sierra San Pedro Martir, northern Lower California, where adherent to the live-oak association of the Upper Sonoran life-zone. There are twelve specimens at hand, one from San Antonio Ranch, at 2100 feet altitude on the upper Santo Domingo River, one from La Joya [La Jolla], 6200 feet altitude, and ten from Concepcion, 6000 feet altitude.

*Measurements*.—See accompanying table.

### ***Baeolophus inornatus sequestratus*, new subspecies**

Oregon Plain Titmouse

*Type*.—Male; no. 46163, Mus. Vert. Zool.; Eagle Point, Jackson County, Oregon; November 26, 1925; collected by William E. Sherwood.

*Distinguishing characters*.—Differs from *Baeolophus inornatus inornatus*, to which it is nearest geographically, in slightly smaller size and in grayer, more leaden color throughout, with but a trace of the brownish tinge that shows clearly on the upper parts of *inornatus*; lower surface less purely white, more suffused with gray. Similar to *B. i. griseus*, but smaller, with especially shorter tail, and darker in color, much less ashy in tone. Similar to *B. i. affabilis* but bill much smaller, and coloration not quite so deeply leaden, especially as to wing and tail feathers.

*Range*.—There are at hand fifteen specimens from Jackson County, Oregon, fourteen from Eagle Point, and one from Ashland. These points are in southwestern Oregon, in the upper Rogue River Valley, between the Coast Range and the Cascades. We have also four specimens from the vicinity of Bogus, Siskiyou County, California, but a short distance south of the California-Oregon boundary line. *Sequestratus* has, apparently, but a limited range; it probably extends little, if at all, beyond the confines of the two counties designated. On the south it is nearly or quite cut off from the habitat of *inornatus* by a broad expanse of mountains, Transition zone and higher. On the east a somewhat wider separation, by coniferous forest or sagebrush plain, obtains between the ranges of *sequestratus* and *griseus*.

*Measurements*.—See accompanying table.

*Remarks*.—Careful examination of the Museum's series of all the races here concerned has convinced us that both the Lower California and Oregon forms are deserving of names. It is a curious fact that, though the intervening forms are different from either, these two subspecies, so far apart geographically, should be strikingly alike in the matter of their relatively dark, brown-less coloration. The outstanding difference between them lies in the bill. The Oregon bird is smaller billed even than typical *inornatus*; the San Pedro Martir race is large billed, like *murinus*.

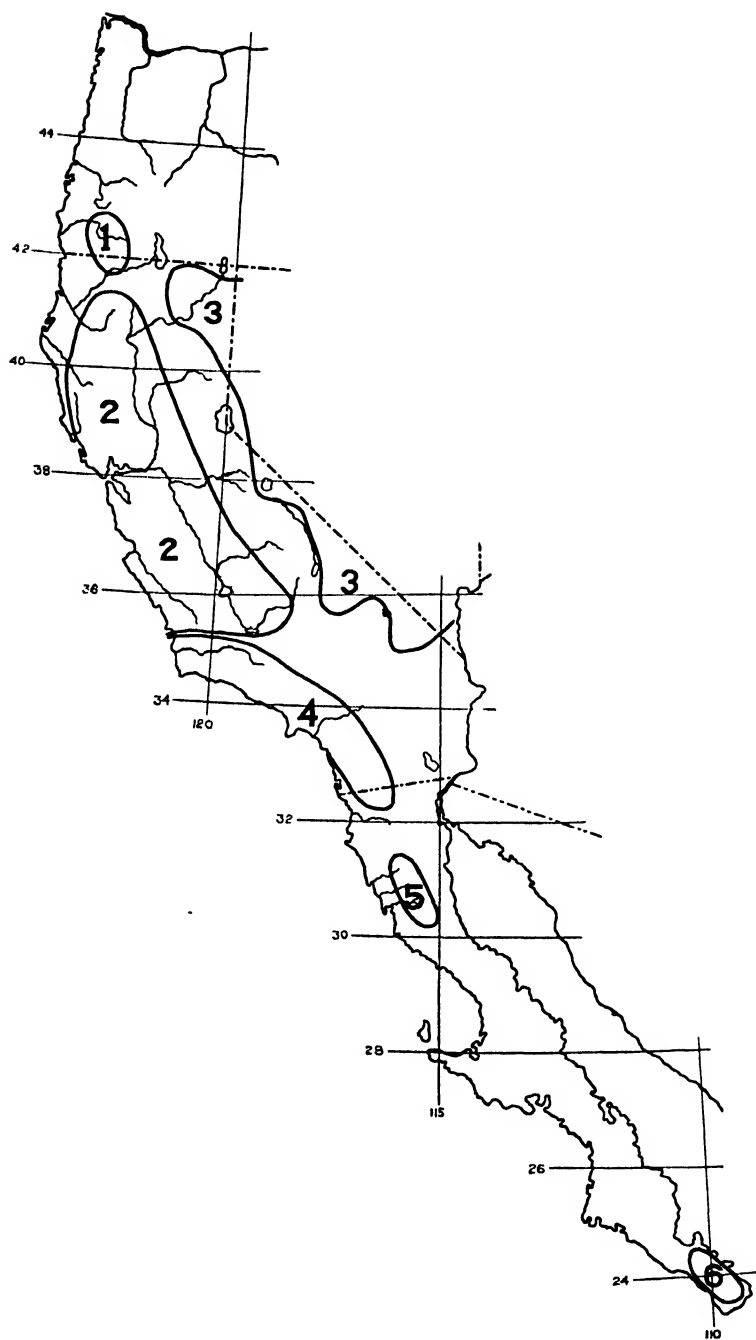


Fig. 1. Map showing approximate distribution of the Plain Titmouses (genus *Baeolophus*) along the Pacific Coast. For names of the subspecies, see text, p. 168.

The present ascription of a race of the Plain Titmouse to southern Oregon is apparently a definite extension northward of the known range of the species. There appears to be but one previously published reference to the occurrence of this bird in Oregon, one specimen having been reported from Ashland (Henninger, 1920, p. 594).

From the San Pedro Martir Mountains a form of Plain Titmouse has been recorded before, by Mr. A. W. Anthony (1893, p. 246). The fact that Anthony identified his specimens as *griseus* rather than *inornatus* is significant as indicating the difference in appearance between the San Pedro Martir birds and those from upper California. The Cape San Lucas subspecies, *Baeolophus inornatus cineraceus*, hardly needs special comment in this connection. In coloration, as contrasted with the San Pedro Martir subspecies, the Cape form lies at an opposite extreme, of ashy pallor. *Cineraceus* is isolated in the mountains of the Cape region, far removed from any other form of the species (see accompanying map).

*Baeolophus inornatus griseus* occurs in California at a few scattered localities near the Nevada line, in extreme northeastern California and in certain desert mountain ranges of the east-central part of the State (see Grinnell, 1923, p. 136). It approaches the range of the Oregon Plain Titmouse fairly closely, and there are places where it still nearer approaches the habitat of *inornatus*; but in each case the nature of the intervening territory is such as to render it highly improbable that there is actual meeting, and consequent intergradation, of these subspecies at any point.

The Pacific Coast races of the Plain Titmouse, according to our analysis of the materials at hand, now stand as follows, listing them from north to south. The approximate territory occupied by each is shown on the accompanying map (fig. 1).

1. *Baeolophus inornatus sequestratus* Grinnell and Swarth. Oregon Plain Titmouse.
2. *Baeolophus inornatus inornatus* (Gambel). California Plain Titmouse.
3. *Baeolophus inornatus griseus* (Ridgway). Gray Plain Titmouse.
4. *Baeolophus inornatus murinus* Ridgway. San Diego Plain Titmouse.
5. *Baeolophus inornatus affabilis* Grinnell and Swarth. San Pedro Martir Plain Titmouse.
6. *Baeolophus inornatus cineraceus* (Ridgway). Ashy Plain Titmouse.

***Psaltriparus minimus melanurus*, new subspecies**

Black-tailed Bush-tit

*Type*.—Male adult; no. 46502, Mus. Vert. Zool.; San José, 2500 feet altitude, lat. 31°, Lower California, Mexico; October 21, 1925; collected by J. Grinnell; original no. 6578.

*Distinguishing characters*.—As compared with *Psaltriparus minimus minimus*, of southern California, of darker, more plumbeous general coloration. In *minimus* there is a brownish tinge to the plumage, above and below, that is lacking in *melanurus*. This difference is most outstandingly apparent on wings and tail; *melanurus* is, comparatively speaking, a "black-tailed" bush-tit.

*Range*.—The following 19 specimens are at hand, all from northern Lower California: La Grulla, 7200 feet altitude, 3; San José, 2500 feet altitude, 10; Valladares, 2700 feet altitude, 2; San Ramon, near sea level at mouth of Santo Domingo River, 4. The area indicated lies on the Pacific slope from the crest of the Sierra San Pedro Martir to the sea. Life-zone chiefly Upper Sonoran, but locally or sporadically Transition and Lower Sonoran.

*Remarks*.—The color differences distinguishing *melanurus* and *minimus* are readily apparent in fresh plumaged birds. Bush-tits change rapidly in appearance with wear and fading of the feathers, and worn-plumaged individuals of these two subspecies no longer exhibit the differences that are so easily seen in early fall. *Melanurus* in its dark slaty color is readily distinguished at any season from the paler subspecies, *P. m. californicus*; and it is, of course, as readily told from the still paler species, *P. plumbeus*. There are specimens of bush-tits at hand from Jackson County, Oregon, perhaps best considered intermediate between *minimus* and *californicus*, which are curiously similar to *melanurus* in appearance, thus paralleling conditions as we find them in the species *Baeolophus inornatus*. In each case the Oregon birds are distinctly dark colored, and of almost, but not quite, the same shade as the Lower California birds.

***Chamaea fasciata canicauda*, new subspecies**

San Pedro Martir Wren-tit

*Type*.—Male adult; no. 46510, Mus. Vert. Zool.; La Grulla, 7200 feet altitude, Sierra San Pedro Martir, Lower California, Mexico; October 8, 1925; collected by J. Grinnell; original no. 6443.

*Distinguishing characters*.—Pale colored as regards plumage, more so even than its nearest geographic relative, *henshawii*, hence the palest colored of the forms of *Chamaea fasciata*. The differences distinguishing *canicauda* from *henshawii*, though slight (hardly appre-



ciable in badly worn plumage) are, it seems to us, notable in being of a different sort from those distinguishing *henshawii* from *C. f. fasciata*. In the latter case, while *henshawii* is much paler than *fasciata*, they are both brown tinged birds. In *canicauda* the browns are almost eliminated. The cinnamon of the underparts is extremely pale, the middle of the belly being nearly white, the upperparts, whole head, wings, and flanks are slaty, while the tail is deep slate. In *canicauda* the bill and feet are unequivocally black; in all the other races of *Chamaea* the bill and feet are more or less tinged with brown—"horn color."

*Range*.—A total of 32 specimens of *canicauda* are available from the following points, all in the Sierra San Pedro Martir or in the territory lying thence westerly to the sea, in northern Lower California. Colnett, 1; San Ramon, mouth of Santo Domingo River, 5; Arroyo Nuevo York, 15 miles south of Santo Domingo, 1; San Telmo, 600 feet, 3; Valladares, 2700 feet, 2; Aguaje del Sauce, 2600 feet, six miles northwest of Valladares, 1; San José, 2500 feet, 4; Concepcion, 6000 feet, 1; La Grulla, 7500 feet, 9; near Vallecitos, at 7500 feet, 3; El Cajon Cañon, 3200 feet, east base of San Pedro Martirs, 2. The species belongs to the chaparral association, most abundant in the Upper Sonoran life-zone, but present also within the Transition and Lower Sonoran life-zones.

*Remarks*.—Geographic variation within the species *Chamaea fasciata* consists, in so far as we can discern, entirely of modifications in tones of color. The total range of variation in this regard involves about as great differences as are to be found within any western species. But although birds from the two extremes of the wren-tit's range, as well as others from certain interlying localities, are easily distinguishable, there is difficulty in defining exact boundaries to the range of any of the described subspecies, due to the gradualness in which color changes are effected between the adjacent regions. There is hardly another bird species in California of continuous distribution throughout the State which exhibits such perfect and evenly graded continuity of color tones between the extremes. Under the circumstances, boundary lines between subspecies can be drawn only more or less arbitrarily; in other words, their exact positions as placed by different systematic workers are likely to vary considerably. In connection with the description of the Lower Californian subspecies here newly named we have taken occasion to go over the entire series of *Chamaea fasciata* in this Museum (some 500 specimens all told) with a view to ascertaining how nearly the features of this large series might be found to agree with definitions, in current use, of the recognized subspecies of this bird.

*Parus fasciatus* was described by Gambel (1845, p. 265) with no exact locality stated, and with no clue given either then or subsequently to indicate whence the type specimen came (see Ridgway, 1904, p. 687, footnote c). *Chamaea fasciata henshawi* was described by Ridgway (1882, p. 13) as a pale colored race from the "interior of California, including western slope of Sierra Nevada," with casual mention of specimens from Walker's Basin, later designated as the type locality of the subspecies. In this paper "var. *fasciata*" is definitely restricted to the "coast of California, south to Sta. Clara, north to or beyond Nicasio."

So the races of the wren-tit stood until Osgood (1899) published his description of *Chamaea fasciata phaea*, type locality Newport, Yaquina Bay, Oregon. Osgood's contention was that Gambel's bird came from southern California, hence that *henshawi* is a synonym of *fasciata*. His division of the species, again into two forms, allots *fasciata* to the inner valleys of California and to the coast region from San Francisco Bay southward. To *phaea* is ascribed a habitat along the coast from San Francisco Bay northward into Oregon.

Osgood's arguments were accepted by Grinnell (1900, p. 85), who, however, considered that the bird from the San Francisco Bay region dismissed by Osgood as intermediate between the two subspecies he recognized, is deserving of formal naming. Grinnell calls it, accordingly, *Chamaea fasciata intermedia*, with the type locality at Palo Alto, Santa Clara County.

By a further division Ridgway (1903, p. 109) applies the name *Chamaea fasciata rufula* to the race from the "central coast district of California, in Marin, San Francisco, and Santa Clara counties," with type locality at Nicasio, Marin County. In a later publication Ridgway (1904, pp. 683-691) makes his position clearer. In reply to Osgood's arguments he affirms that Gambel's name *fasciata* applies to the bird from the south and east sides of San Francisco Bay (*intermedia* of Grinnell), and that therefore the name *henshawi* is, as originally stated, applicable to the pale-colored race from interior and southern California.

Careful consideration of the facts in the case, together with study of the quite adequate series of skins in this Museum, leads us to conclusions in agreement with those of Ridgway, in nearly every detail. Our course of reasoning is as follows:

Some few years ago the senior author examined Gambel's type (and only known) specimen of *Chamaea fasciata* (no. 3339, U. S. Nat. Mus.). His notes, made at the time, upon this specimen read in part as follows: "Most nearly (and I may say, quite accurately) resembles skins from the vicinity of Monterey. Type in fairly good condition, but I should judge yellowed by age. Gambel never gave any clue as to where his wren-tits came from, but judging from the type itself, as well as from the fact that many other of his birds *were* taken there, I feel secure in placing Monterey as the type locality. Birds from Santa Cruz, Santa Clara, and San Mateo counties are decidedly darker."

This Museum has now a satisfactory representation of wren-tits from Monterey, in fresh, unworn plumage. It is true that these birds are, on the average, paler colored than San Francisco Bay specimens; but we do not now believe in the further refinement of using the name *intermedia* for the latter, and we accordingly sink that name into the synonymy of *fasciata*. Monterey birds are sufficiently paler than northern ones to render conceivable the ascription of a bird from that region to the southern California form (as Osgood did the type of *fasciata*); but on the whole Monterey birds certainly are better placed with those from San Francisco Bay than with those from Los Angeles and San Bernardino counties. Osgood's attitude is further understandable by the fact that certain specimens of wren-tit from southern California are appreciably browner than those from the vicinity of the type locality of *henshawi*, darker even than those from the central Sierra Nevada. The boundary line between *fasciata* and *henshawi* on the southern California coast may now be indicated as some distance south of Monterey (see accompanying map).

Another consideration in restricting the type locality of *fasciata* to Monterey is that the principle of "first reviser" may be urged with reason to apply here. For Ridgway was the first to "split" the species into two subspecies and he definitely restricted the application of the name *fasciata*, in a subspecific sense, to the central coast belt of California. Osgood, many years later, had no ground, if this principle be valid, for reversing Ridgway's action.

Disagreement with Osgood as to the application of the names *fasciata* and *henshawi* does not, of course, affect the standing of his subspecies, *phaea*. This is a strongly marked form, but restricted to a more northern habitat than that allotted to it by its describer. In our opinion it does not enter into even extreme northern California;

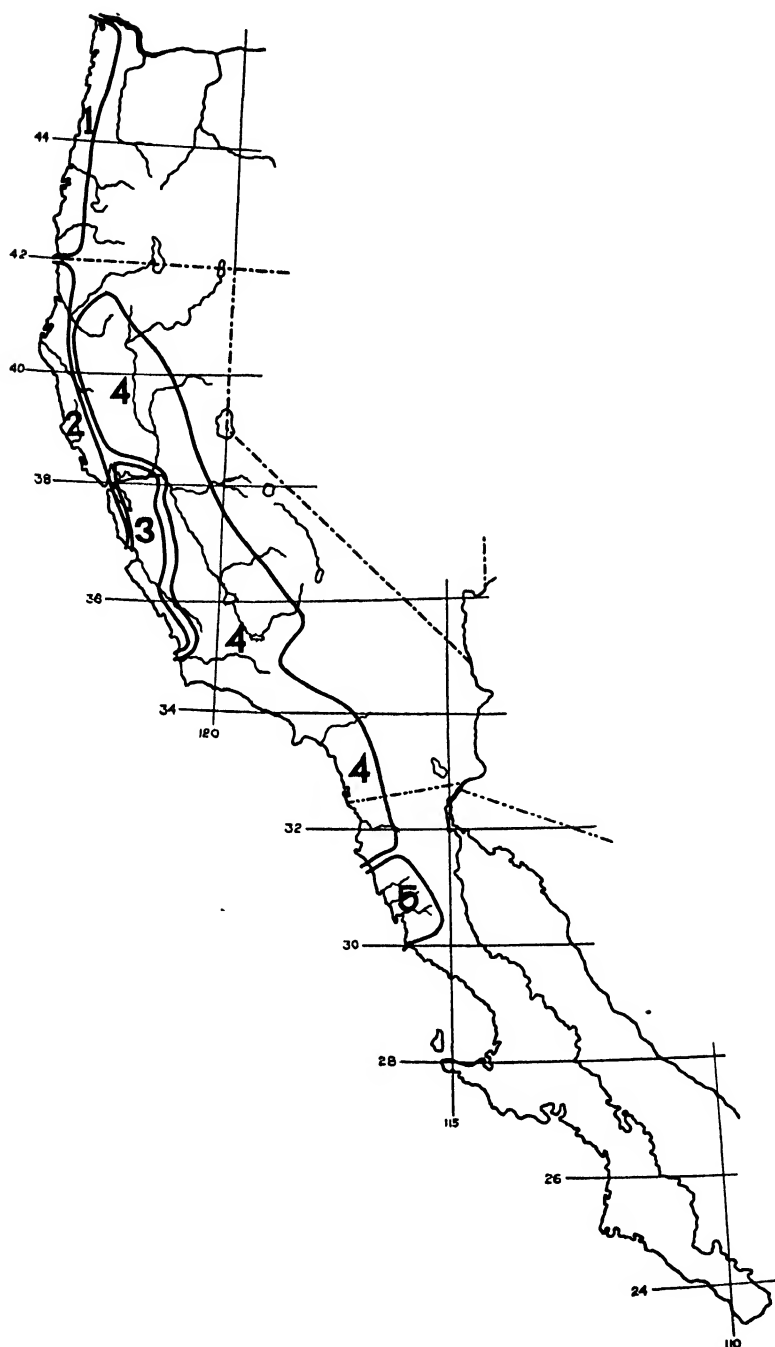


Fig. 2. Map showing approximate distribution of the Wren-tits (genus *Chamaea*). For names of the subspecies, see text, p. 174.

specimens from Humboldt Bay and Crescent City seem to us nearer to *rufula*. Admittedly in rather arbitrary fashion, we are putting the line of merge between *phaea* and *rufula* on the California-Oregon boundary.

There are difficulties, well stated by Osgood (1901), in indicating upon a map the exact distribution of any of the subspecies of the wren-tit, due in most part to the gradualness of the change in characters that takes place over wide areas. Such difficulties are added to in certain regions, such as in Solano and Napa counties, immediately north of San Francisco Bay, and even in the lower Sacramento Valley, where a wren-tit population, exactly similar to *fasciata* in appearance, may owe its characters to intergradation between the dark-colored *rufula* of the coast and the pale-colored *henshawi* of the Sierran foothills, rather than to real and direct affinity with *fasciata* from south of San Francisco Bay.

The races of *Chamaea fasciata* as indicated in the preceding discussion now stand as follows, listing them from north to south. The approximate territorial limits of each are shown on the accompanying map (fig. 2).

1. *Chamaea fasciata phaea* Osgood. Northern Wren-tit.
2. *Chamaea fasciata rufula* Ridgway. Ruddy Wren-tit.
3. *Chamaea fasciata fasciata* (Gambel). Intermediate Wren-tit.
4. *Chamaea fasciata henshawi* Ridgway. Pallid Wren-tit.
5. *Chamaea fasciata canicauda* Grinnell and Swarth. San Pedro Martir Wren-tit.

## LITERATURE CITED

ANTHONY, A. W.

1893. Birds of San Pedro Martir, Lower California. *Zoe*, 4, 228-247.

GAMBEL, W.

1845. Descriptions of new and little known birds, collected in upper California. *Proc. Acad. Nat. Sci. Phila.*, 2, 263-266.

GRINNELL, J.

1900. The intermediate wren-tit. *Condor*, 2, 85-86.  
1908. The southern California chickadee. *Condor*, 10, 29-30.  
1923. The present state of our knowledge of the gray titmouse in California. *Condor*, 25, 135-137, fig. 45.

HENNINGER, W. F.

1920. The plain titmouse a new bird for Oregon. *Auk*, 37, 594.

OSGOOD, W. H.

1899. *Chamaca fasciata* and its subspecies. *Proc. Biol. Soc. Wash.*, 13, 41-42.  
1901. Questions of the day. *Condor*, 3, 50-51.

RIDGWAY, R.

1882. Description of several new races of American birds. *Proc. U. S. Nat. Mus.*, 5, 9-15.  
1903. Description of new genera, species and subspecies of American birds. *Proc. Biol. Soc. Wash.*, 16, 105-112.  
1904. The birds of North and Middle America. *U. S. Nat. Mus. Bull.*, 50, pt. III, xx+801, 19 pls.

*Transmitted August 2, 1926.*



A SYSTEMATIC STUDY OF SOME  
POCKET GOPHERS FROM WESTERN NEVADA

BY  
JOSEPH GRINNELL



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 6, pp. 177-188, plates 9-11

Issued December 10, 1926

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# A SYSTEMATIC STUDY OF SOME POCKET GOPHERS FROM WESTERN NEVADA

BY

JOSEPH GRINNELL

(Contribution from the Museum of Vertebrate Zoology, University of California)

---

The present paper is justified primarily because of the receipt at the Museum of Vertebrate Zoology of some fresh collections of pocket gophers (genus *Thomomys*) which offer facts seemingly new and of importance in the general understanding of this group of 'plastic' rodents. The collections in question were gathered by Annie M. Alexander and Louise Kellogg in course of natural history explorations in western Nevada, and have been presented by them to this Museum. This gathering was not done haphazardly but on a rational plan by which sequestered 'colonies' of pocket gophers were sought out and sampled; for these rodents are by no means continuously distributed over the Great Basin territory. This fact, of discontinuity of range, has, of course, its significance.

At the outset it is in order to state that the exhaustive Revision of the Pocket Gophers of the Genus *Thomomys*, by Vernon Bailey (1915), has served as the starting point, and at many turns the guide, for the following systematic study of these collections.

## ***Thomomys solitarius*, new species**

Solitary Pocket Gopher

*Type*.—Male subadult, skin and skull; no. 36378, Mus. Vert. Zool.; Finger-rock Wash, Stewart Valley, 5400 feet altitude, Mineral County, Nevada; October 9, 1925; collected by Annie M. Alexander and Louise Kellogg; orig. no. 54.

*Characters*.—Apparently a member of the "*Thomomys perpallidus* group" (see Bailey, 1915, pp. 33, 68); size small (males with total length of 205 to 216 millimeters, hind foot 28); sexes not very different in size or proportions, externally or cranially; tail rather long (64 to 73 mm., hence nearly one-third total length, instead of one-fourth); ear small. Coloration pale, buffy not gray; lower surface and whole tail strikingly white. Skull short and brain-case relatively

broad and flat; rostrum short, nasals small; interorbital constriction broad; zygomatic arches not widely spreading; skull smooth, parietal ridging weakly indicated; auditory bullae very large, rounded; all the teeth small, the incisors and the axis of their exposed portions about at right angles to axis of cranium, not either incurved or forward-projecting. For dimensions see accompanying table of measurements, and for certain characters in comparison with those of neighboring and related species see plate 9.

MEASUREMENTS (IN MILLIMETERS) OF *Thomomys solitarius* FROM THE TYPE LOCALITY; TAKEN OCTOBER 9 TO 17, 1925

| M.V.Z.<br>No. | Sex | Age       | Total length | Tail vertebrae | Hind foot | Basilar length<br>Hensel | Length nasals | Zygomatic<br>breadth | Mastoid<br>breadth | Width rostrum<br>at middle | Interorbital<br>breadth | Alveolar length<br>upper molar<br>series |
|---------------|-----|-----------|--------------|----------------|-----------|--------------------------|---------------|----------------------|--------------------|----------------------------|-------------------------|--|
| 36378         | ♂   | subad.    | 205          | 66             | 28        | 31.5                     | 12.4          | 21.7                 | 18.9               | 8.1                        | 6.6                     | 7.8                                      |
| 36384         | ♂   | ad.       | 209          | 68             | 28        | 31.2                     | 12.7          | 22.4                 | 19.1               | 8.2                        | 7.0                     | 7.6                                      |
| 36382         | ♂   | ad.       | 216          | 67             | 28        | 31.9                     | 13.0          | 21.8                 | 19.0               | 8.1                        | 7.2                     | 7.3                                      |
| 36380         | ♂   | subad.    | 215          | 73             | 28        | 31.5                     | 13.0          | 20.9                 | 18.4               | 8.1                        | 6.6                     | 8.1                                      |
| 36381         | ♂   | (?)subad. | 206          | 64             | 28        | 30.3                     | 12.0          | 21.6                 | 18.3               | 7.7                        | 6.5                     | 7.7                                      |
| 36383         | ♀   | subad.    | 203          | 66             | 28        | 30.3                     | 12.0          | 21.0                 | 18.0               | 7.5                        | 6.7                     | 7.8                                      |
| 36379         | ♀   | subad.    | 194          | 58             | 27        | 30.0                     | 12.3          | 20.5                 | 18.7               | 7.0                        | 6.6                     | 7.5                                      |

*Distribution.*—Known only from the type locality (see pl. 11). This is a dry, Upper Sonoran mesa.

*Comparisons and relationships.*—As within his "*Thomomys perpallidus* group," Bailey (1915, pp. 68–80) recorded from Nevada only the races *T. p. perpes*, *T. p. canus*, and *T. p. aureus*. Of these, the range of *canus* as assigned by him (*op. cit.*, p. 73, map, fig. 5) is the only one that comes anywhere near to the type locality of the form I now name *solitarius*. Thus, naturally, when the new Nevada material came in, as soon as I had eliminated the possibility of its association with any other group, such as the fossor, monticola, or townsendii group, I proceeded to make close comparison with *T. p. canus*, with results as follows.

The resemblances between *canus* and *solitarius* externally lie mainly in small ear, relatively long tail, and generally pallid coloration. But the differences are marked—in decidedly smaller size of *solitarius*, in its smaller feet and weaker fore claws, its buffy instead of decidedly ashy gray tone of coloration, and in its whiter lower surface and white tail. This ventral whiteness of *solitarius*, involving shortening of the neutral gray at the bases of the hairs, as well as also its elimination altogether on the wrists and ankles, is duplicated among pocket gophers only in *perpallidus* and *albatrus*, of the Colorado Desert.

Then cranially, while *solitarius* shows resemblance to *canus* in certain 'group' characters, it is sharply different in its short rostrum, with commensurately short nasals and premaxillary tongues, in its narrow zygomatic spread, in its weak dentition (notably the small stubby incisors), and in such details as slenderer and less broadly diverging hamular processes. Indeed, the differences between these

two forms are so great that I cannot consider intergradation between them possible at the present time, especially in view of the nearness of record-stations of *canus* (for example, Cloverdale, Nye County). In other words *solitarius* is very unlikely to be found to link up with *canus* by geographic intergradation. Its relationships probably lie much more closely with some more distantly situated form.

A form, *melanotis*, was described by the present writer (1918, p. 425), subsequently to the appearance of Bailey's monograph, from the White Mountains, just over the State line from Nevada, in Mono County, California. This form, although described as a full species, I now consider one of the intergradient series with *perpallidus*, geographic intergrades between it and *T. p. perpes* having lately come to light. *Solitarius* differs, I find, in quite as great an amount from *melanotis* as from *canus*, but, of course, in different ways. Externally, *solitarius* is the smaller, with longer tail, and buffier color above; it is the whiter below and on the tail, and it has a less extensively and intensively blackish ear-patch. Then the skull of *solitarius* is not only the smaller, but the zygomatic arches spread much less widely, the interorbital constriction is notably less (that is, the breadth of the cranium between the orbits is greater), the parietal ridges are farther apart, the auditory bullae are shorter and more rounded, the teeth are smaller, and the incisors do not project forward. These differences are so great in aggregate amount as to make direct, present-day continuity between *solitarius* and *melanotis* quite improbable.

Then there is *Thomomys perpallidus perpes*, of the lower portion of Owens Valley, a little farther away, in Inyo County, California, nearer in general size, but from which *solitarius* differs as follows: ears and feet smaller, color tone above less strongly fulvous and below whiter, and there is more black back of ear; skull with less widely spreading zygomata, and shorter rostrum; nasals broader posteriorly, parietal ridges less closely approaching, auditory bullae larger and rounder, molariform teeth smaller, and incisor teeth much shorter, narrower, and not incurved.

There is a gopher, named by Elliot (1903, p. 248) from the Panamint Mountains, Inyo County, California, which Bailey (1915, p. 72) synonymizes under *perpes*, but which I consider, on the basis of adequate series recently acquired by the Museum of Vertebrate Zoology, to be a very good form. This is *Thomomys scapterus*. *Solitarius* resembles this species rather more closely, in some respects, than it does *perpes*, for example in similar size, weak dentition, and narrowly spreading zygomata; but notable differences also obtain, as follows: *Solitarius* is very much paler colored, both above and below, and it has smaller ears; its skull possesses broader rostrum, longer nasals, greater interorbital breadth, more nearly parallel zygomata (not converging anteriorly), more inflated auditory bullae, and longer incisors. The rostrum of *scapterus* is notably weak, with the nasals very short, these features setting it off sharply from all other gophers of the *perpallidus* group. I do not think the immediate relationships of *solitarius* lie with *scapterus*.

Comparison with still more distantly located races, such as *aureus*, *amargosae*, *operarius*, and *mohavensis*, brings no more decisive evi-

dence as to the immediate relationships of *solitarius*. All that can be said in conclusion is that this new form is at the present day a seemingly disconnected and a rather far differentiated member in the *perpallidus* series.

### **Thomomys falcifer, new species**

Sickle-toothed Pocket Gopher

*Type*.—Male adult, skin and skull; no. 35043, Mus. Vert. Zool.; Bell's Ranch, 6890 feet altitude, Reese River Valley, Nye County, Nevada; June 3, 1925; collected by Annie M. Alexander; orig. no. 15.

*Characters*.—A member of the "*Thomomys fossor* group" (see Bailey, 1915, pp. 33, 111); size medium (adult males with total length of 213 to 223 millimeters, hind foot 26 to 28); tail rather short (52 to 59 mm.); ear small. Coloration rather dark (above, dull verona brown [of Ridgway, 1912], beneath, deep neutral gray thinly overwashed with very pale drab-gray). Skull with long and very narrow rostrum; nasals long and, in dorsal view, constricted at middle; premaxillary tongues, as seen from above, very much narrowed posteriorly; parietal ridges well developed but remaining (with advancing age) far apart and parallel throughout their lengths, not converging where the parietals meet; incisor teeth exceedingly long, somewhat forward-projecting, and markedly curved (sickle-shaped in lateral profile). Difference in size between mature male and female is great; but the main cranial as well as external characters are apparent in both sexes, save less accentuated in some respects in the female. For dimensions in both sexes, see accompanying table of measurements, and for characters in comparison with neighboring or related species, see plate 10.

MEASUREMENTS (IN MILLIMETERS) OF *Thomomys falcifer* FROM THE TYPE LOCALITY; TAKEN JUNE 1 TO 5, 1925

| M. V. Z. No.    | Sex | Age     | Total length | Tail vertebrae | Hind foot | Basilar length Hensel | Length nasals | Zygomatic breadth | Mastoid breadth | Width rostrum at middle | Interorbital breadth | Alveolar length upper molar surface |
|-----------------|-----|---------|--------------|----------------|-----------|-----------------------|---------------|-------------------|-----------------|-------------------------|----------------------|-------------------------------------|
| 35035           | ♂   | ad      | 217          | 56             | 27        | 34 1                  | 14 3          | 24 5              | 19 5            | 7 9                     | 6 7                  | 8 0                                 |
| 35036           | ♂   | ad      | 213          | 54             | 27        | 34 0                  | 14 4          | 23 2              | 18 9            | 7 5                     | 6 6                  | 7 7                                 |
| 35042           | ♂   | old ad. | 213          | 52             | 27        | 34 8                  | 14 3          | 24 1              | 19 7            | 7 4                     | 6 7                  | 7 9                                 |
| 35043           | ♂   | old ad. | 218          | 56             | 27        | 34 6                  | 14 7          | 24 8              | 20 3            | 7 4                     | 6 8                  | 8 1                                 |
| 35046           | ♂   | ad.     | 222          | 56             | 27        | 33 8                  | 12 6          | 23 1              | 19 2            | 7 7                     | 6 6                  | 7 3                                 |
| 35047           | ♂   | ad.     | 221          | 57             | 26        | 34 0                  | 13 6          | 23 0              | 18 8            | 7 6                     | 6 1                  | 7 4                                 |
| 35049           | ♂   | old ad. | 223          | 59             | 28        | 34 4                  | 15 6          | 25 6              | 20 6            | 7 8                     | 6 7                  | 7 8                                 |
| 35050           | ♂   | subad.  | 209          | 56             | 27        | 32 1                  | 13 8          | 23 0              | 18 8            | 7 8                     | 6 3                  | 7 4                                 |
| Average of 8 ♂♂ |     |         | 217          | 56             | 27        | 34 0                  | 14 2          | 23 9              | 19 5            | 7 6                     | 6 6                  | 7 7                                 |
| 35037           | ♀   | old ad. | 218          | 58             | 27        | 31 0                  | 12 9          | 22 0              | 17 9            | 7 5                     | 7 1                  | 7 5                                 |
| 35039           | ♀   | subad.  | 193          | 56             | 26 5      | 29 5                  | 11 3          | 20 3              | 17 8            | 6 6                     | 6 2                  | 7 3                                 |
| 35040           | ♀   | ad.     | 203          | 58             | 26        | 29 3                  | 11 8          | 20 2              | 17 6            | 6 4                     | 6 3                  | 7 1                                 |
| 35041           | ♀   | old ad. | 187          | 44             | 26 5      | 30 2                  | 12 7          | 21 5              | 17 9            | 6 7                     | 7 2                  | 7 6                                 |
| 35045           | ♀   | subad.  | 195          | 56             | 26        | 29 1                  | 11 7          | 20 4              | 17 1            | 6 9                     | 6 3                  | 6 6                                 |
| 35052           | ♀   | ad.     | 186          | 53             | 25        | 29 1                  | 12 6          | 20 1              | 16 8            | 6 4                     | 6 1                  | 7 6                                 |
| 35053           | ♀   | subad.  | 189          | 52             | 25        | 29 2                  | 11 6          | 20 5              | 17 0            | 6 7                     | 6 2                  | 7 3                                 |
| 35054           | ♀   | subad.  | 182          | 49             | 25        | 28 5                  | 10 8          | .                 | 17 3            | 7 0                     | 6 3                  | 6 8                                 |
| Average of 8 ♀♀ |     |         | 194          | 53             | 25 9      | 29 5                  | 11 9          | 20 9              | 17 4            | 6 8                     | 6 5                  | 7 2                                 |

*Distribution*.—Known so far only from the type locality, as given above.

*Comparisons and relationships*.—The geographic position of the form here newly named, lying between the Rocky Mountains where *Thomomys fossor* and near-related forms exist and the western margin of the Great Basin where *Thomomys quadratus* and its subspecies occur, points out the sort of comparisons logically to be made. Taking the members of the "fossor group" from west to east the following differences are in evidence, the likenesses being those common to the group as pointed out by Bailey (*op. cit.*).

From *T. quadratus quadratus*, *T. falcifer* differs slightly in external features—in paler, less russet more tawny tone of coloration above, in less deeply plumbeous tone of basal parts of pelage beneath, with whitish rather than buffy overwash, and in shorter tail. Cranially, the differences so far as shown by materials in hand and by Bailey's figures and diagnoses are as follows: In *falcifer* as compared with *quadratus* from Modoc County, California, the skull in males is as a whole larger; the rostrum averages longer and narrower; the parietal ridges are more pronounced and more constantly parallel; the auditory bullae are larger; and the incisor teeth are much longer, hence relatively slenderer, and they are much more curved in lateral profile. Females of the two forms differ similarly but in lesser degree.

From *T. quadratus fisheri* (series from Mono County, California), *falcifer* differs externally in somewhat larger size, and in darker tones of coloration both above and below. Cranially the differences are more pronounced and they appear to be constant, as follows: in male *falcifer*, as compared with male of *fisheri* of equal age, the skull as a whole is decidedly larger; the rostrum is longer and hence relatively slenderer; there is greater basal constriction of rostrum, with resultant narrowing of premaxillary tongues; the nasals are longer and usually show a distinct in-swing of lateral margins, producing an hourglass shape in dorsal view; the zygomatic arches are more wide-spreading; the parietal ridges are more prominent; the auditory bullae are larger; and the incisor teeth are much longer, and they are more forward-projecting. Females share in most of these differences but exhibit them in lesser degree.

Gophers from the Pine Forest Mountains, Humboldt County, Nevada, north of the Humboldt River valley (see Taylor, 1911, p. 258), while slightly different from *fisheri* from Mono County, California, are still to be called *fisheri*; the slight departures they show do not tend to bridge the gap between typical *fisheri* and *falcifer*, the type locality of the latter lying south of the Humboldt River valley, which valley is inhabited by the altogether different sort of gopher, *Thomomys townsendii nevadensis* (see Grinnell, 1926, p. 4).

Passing now to the eastward, and making comparison, first, with *Thomomys fossor*, of western Colorado and parts of Wyoming and Utah, *falcifer* is found to present considerable differences. While the only external departures in *falcifer* are in smaller ear and paler tones of color, cranially it is so very different from *fossor* as scarcely to need comparison; notable departures are in the larger size of the skull of the former, the much broader brain-case and zygomatic spread,

the parallel instead of posteriorly diverging parietal ridges, the heavier molariform teeth, and especially the much longer and more forward projecting incisors.

There remain in the "fossor group," only *T. bridgeri* and *T. uinta*, the former inhabiting parts of Wyoming and Idaho, the latter inhabiting other parts of Wyoming and Idaho and parts of Utah (see Bailey, 1915, pp. 23, 37, 112, 113, pl. 7). Externally *falcifer* differs from *bridgeri* in much lesser size, in smaller ear, and in more weakly clawed front foot. Cranially, the differences are emphatic, as follows: in *falcifer*, smaller general size, slenderer rostrum, shorter nasals with hourglass outlines, nasals ending truncately behind instead of emarginate, brain-case less angular, parietal ridges parallel instead of converging, and incisors much slenderer. *Falcifer* is more nearly the general size of *uinta* but differs from the latter sharply as follows: ears, and claws of forefeet, markedly smaller; coloration both above and below paler, less deeply brown; skull with rostrum deeper; bullae longer, less rounded; posterior tips of nasals truncate rather than emarginate; interorbital width less; parietal ridges better marked and more uniformly parallel; interparietal bone triangular rather than pentagonal; and incisors in males longer. Also the difference in size between the sexes is decidedly greater in *falcifer* than in *uinta*.

Bailey (*op. cit.*, p. 116) suggests that *fisheri* in central Nevada "perhaps grades into *uinta*." The form I name *falcifer* might possibly be interpreted broadly as providing such an intergradient step. But scrutiny of its cranial features shows important departures from both *fisheri* (or *quadratus*) and *uinta* (or *bridgeri* or *fossor*), as set forth in the statement of "Characters" above. Of course it does remain probable that future collecting will bring further indication of near relationships among the members of the *fossor* group; but because of the interrupted conditions, from a gopher-distribution standpoint, perfect continuity of populations and complete interblending of races spatially are unlikely. Indeed, several more definable forms probably await naming.

## LITERATURE CITED

BAILEY, V.

1915. Revision of the pocket gophers of the genus *Thomomys*. U. S. Dept. Agr., Bur. Biol. Surv., N. Am. Fauna, 39, 136 pp., 8 pls., 10 figs. in text.

ELLIOT, D. G.

1903. Descriptions of twenty-seven apparently new species and subspecies of mammals, all but six collected by Edmund Heller. Field Columb. Mus., Zool. Ser., 3, 239-261.

GRINNELL, J.

1918. Six new mammals from the Mohave Desert and Inyo regions of California. Univ. Calif. Publ. Zool., 17, 423-430.
1921. Two new rodents (genera *Thomomys* and *Marmota*) from the eastern border of California. Univ. Calif. Publ. Zool., 21, 239-244, 6 figs. in text.
1926. The pocket gopher of Honey Lake Valley. Univ. Calif. Publ. Zool., 30, 1-6, pl. 1.

RIDGWAY, R.

1912. Color standards and color nomenclature (Washington, published by the author), 8 + 44 pp., 53 col. pls.

TAYLOR, W. P.

1911. Mammals of the Alexander Nevada Expedition of 1909. Univ. Calif. Publ. Zool., 7, 205-307.

*Transmitted September 17, 1926.*



## EXPLANATION OF PLATES

### PLATE 9

Views, not re-touched, of skulls of five species of the "Thomomys perpallidus group" of pocket gophers. All photographed natural size.

*a*, *Thomomys perpallidus perpes*, ♂, no. 16844, Mus. Vert. Zool.; Lone Pine, Inyo County, California; April 12, 1912; H. A. Carr.

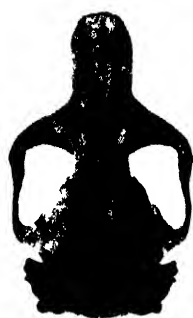
*b*, *g*, *Thomomys solitarius*, ♂, no. 36378, Mus. Vert. Zool.; Finger-rock Wash, Mineral County, Nevada; October 9, 1925; A. M. Alexander and L. Kellogg.

*c*, *h*, *Thomomys perpallidus canus*, ♂, no. 36375, Mus. Vert. Zool.; West Walker River, Lyon County, Nevada; October 31, 1925; A. M. Alexander.

*d*, *Thomomys perpallidus melanotis*, ♂, no. 26503, Mus. Vert. Zool.; White Mountains, Mono County, California; July 27, 1917; J. Grinnell.

*e*, *Thomomys solitarius*, ♀, no. 36379, Mus. Vert. Zool.; Finger-rock Wash, Mineral County, Nevada; October 9, 1925; A. M. Alexander and L. Kellogg.

*f*, *Thomomys scapterus*, ♂, no. 26459, Mus. Vert. Zool.; Panamint Mountains, Inyo County, California; May 31, 1917; J. Dixon.



*a*



*b*



*c*



*d*



*e*



*f*



*g*



*h*

## PLATE 10

Views, not re-touched, of skulls of four species of the "Thomomys fossor group" of pocket gophers. All photographed natural size.

*a, g, Thomomys quadratus fisheri*, ♂, no. 7852, Mus. Vert. Zool.; Pine Forest Mountains, Humboldt County, Nevada; July 9, 1909; W. P. Taylor and C. H. Richardson, Jr.

*b, h, Thomomys falcifer*, ♂, no. 35043, Mus. Vert. Zool.; Reese River, Nye County, Nevada; June 3, 1925; A. M. Alexander.

*c, Thomomys bridgeri*, ♂, no. 2713, Mus. Vert. Zool.; Fort Bridger, Wyoming; August 10, 1908; C. L. Camp.

*d, Thomomys quadratus fisheri*, ♂, no. 23193, Mus. Vert. Zool.; Walker Lake, Mono County, California; September 14, 1915; W. P. Taylor.

*e, Thomomys falcifer*, ♀, no. 35052, Mus. Vert. Zool.; Reese River, Nye County, Nevada; June 5, 1925; A. M. Alexander.

*f, Thomomys quadratus fisheri*, ♀, no. 23197, Mus. Vert. Zool.; Walker Lake, Mono County, California; September 15, 1915; W. P. Taylor.



*a*



*b*



*c*



*d*



*e*



*f*



*g*



*h*

## PLATE 11

*a*, Finger-rock Wash, Stewart Valley, Mineral County, Nevada; altitude 5400 feet; life-zone, Upper Sonoran. This is the type locality of *Thomomys solitarius*, the burrows of which were far scattered in the sandy soil among the xerophilous shrubs.

*b*, As above, an adjacent segment of the landscape, looking northwest. Photos taken October 17, 1925.

The dominant perennial plants in this vegetational association are as follows: *Chrysothamnus nauseosus*, *Artemisia tridentata*, *Atriplex confertifolia*.



*a*



*b*



AN OUTBREAK OF HOUSE MICE  
IN KERN COUNTY, CALIFORNIA

BY  
F. RAYMOND HALL



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 7, pp. 189-203

Issued February 21, 1927

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# AN OUTBREAK OF HOUSE MICE IN KERN COUNTY, CALIFORNIA

BY  
E. RAYMOND HALL

(Contribution from the Museum of Vertebrate Zoology, University of California)

## CONTENTS

|                             | PAGE |
|-----------------------------|------|
| Introduction .....          | 189  |
| Description of region ..... | 190  |
| Time of outbreak .....      | 190  |
| Source of the mice .....    | 190  |
| Numbers of mice .....       | 192  |
| Economic bearings .....     | 194  |
| Biological inferences ..... | 196  |

## INTRODUCTION

There was received at the Museum of Vertebrate Zoology, on January 10, 1927, from Mr. Claude Gignoux of Berkeley, the following information sent to him by a correspondent from Taft, Kern County, California: "Talk about 'nothing new under the sun.' Well there is. The highway between Panama and Taft is literally plastered with dead mice, and millions of them alive chasing across the highway; it's sickening. They say the Honolulu Co. killed 4 tons of mice."

This and other reports of similar tenor led the Director of the Museum to delegate the writer to make an investigation with the object of securing a first-hand record of the facts in regard to the outbreak, its biological history, and its economic implications, if any. Accordingly, the writer arrived in Bakersfield on January 13, 1927, where he was immediately put in touch with local conditions by Mr. Whit. C. Barber, Kern County Horticultural Commissioner, and Mr. C. H. Bowen, also of the Horticultural Commission.

Investigation from January 13 to 16, inclusive, verified the reports previously received at the Museum of Vertebrate Zoology. The mice were house mice (*Mus musculus*). The affected area was found to be about eighteen miles in diameter and the mice were found to have come from, and still to be coming from, the dry bed of Buena Vista Lake.

## DESCRIPTION OF REGION

Buena Vista Lake, which lies at the center of the affected area, is situated seventeen miles southwest of Bakersfield, Kern County, California, in the southern end of the San Joaquin Valley. The country around the lake is in the arid Lower Sonoran Life Zone. North and south of the lake the barren hills support few or no human inhabitants; but west of the lake there are rich oil and gas deposits, and here large numbers of people are concentrated in small towns and camps on, and in the immediate vicinity of, the various oil companies' properties. East of the lake the reclaimed land, which previous to 1909, was part of Buena Vista Lake, is largely cultivated, barley, wheat, kafir corn, and cotton being the principal crops.

## TIME OF OUTBREAK

In the invaded area outside the Buena Vista Lake basin the first appearance of the mice in impressive numbers is said to have been in the latter part of November, 1926. A second, smaller, invasion was reported in December. The mice continued to be present in large numbers until January 6, 1927, when a third marked invasion took place. The house mice continued to invade the country around Buena Vista Lake until January 15. On this date, according to reports from numerous persons that lived near, or chanced to be near, the lake margin, and confirmed by the writer's personal investigation of the eastern and western sides of the lake, there was a lull.

## SOURCE OF THE MICE

Originally, Buena Vista Lake was fed by the Kern River; but the lake basin, comprising thirty-five square miles, now is dry and has been so for the past three years. All the land in this area, except a narrow strip along the north side of the lake, was planted to barley two years ago. Last year about one-half the area was planted to kafir corn and the remainder allowed to come up in volunteer barley. Fallen barley and kafir corn, and that which shattered to the ground in the harvesting of the crops, provided abundant food for mice;

in addition the kafir corn from which the heads were cut may have provided shelter from enemies and safe breeding-places for the mice. During the past fall and winter, sheep were grazed over the area and thus was destroyed the cover that sheltered the mice, while at the same time, between the mice and the sheep, the available food was mostly eaten up. Certainly no visible food of a nutritious character for the house mice existed on the parts of the lake basin visited by the writer. When the over-abundant mouse population of this dry lake bed was deprived of food and shelter, a peripheral, or radial, migration resulted, and the territory on every side of the lake was invaded.

Evidence that the mice came from the dry lake bed is as follows:

1. Food and shelter for house mice existed, in quantity, in the lake bed and at no other point in the now invaded area north, west, or south of the lake.

2. The mice first appeared in the territory surrounding the lake (excepting that territory east of the lake which is dealt with below) only after the food and shelter in the lake basin had mostly been destroyed.

3. Shepherders tending flocks in the lake basin, and other persons having occasion to go there, reported vast numbers of mice several months before they appeared in the territory surrounding the lake.

4. Investigation, on January 14, 1927, in the western part of the lake basin revealed more mice per given area there than in the invaded territory outside the lake basin.

5. Collected reports of residents of the invaded area as to the time that the mice reached different ranches, fields, and groups of farm buildings, give direct correlations between distances of points from the lake and the periods of time elapsing between first reports of the outbreak and appearance of the mice at these points.

6. Poisoned wheat placed by Mr. C. H. Bowen for a distance of 400 yards, on both sides of the paved highway that extends along the north side of the lake, netted, during one night, many dead mice on the side of the highway near the lake and few mice on the side farther from the lake; whereas poisoned grain placed along an adjacent and similar stretch of highway but only on the side of the highway away from the lake, netted, at the same time, many mice.

7. A series of four furrows, each having poisoned grain in it, parallel to the margin of the lake and to one another, netted progressively fewer mice from the furrow nearest the lake to the one farthest from the lake.

Although there is definite evidence that the house mice migrated out in every direction from the dry bed of Buena Vista Lake and that nearly all the mice in the invaded area came from there, an excessive number of mice probably came from endemic stock in the cultivated land immediately east of Buena Vista Lake. Within the area not over two miles east of the levee marking the eastern boundary of Buena Vista Lake, there were reports that huge numbers of house mice had been found under grain stacks as early as October, 1926. The land in this region is largely planted to barley, wheat, and kafir corn, and abundant food would seem to have been available there also. However, despite the fact that there was a large endemic population just east of the lake, the numbers, according to report, were almost inconsequential as compared with the numbers present after the migration out of the bed of the lake proper.

### NUMBERS OF MICE

At the source, the dry bed of Buena Vista Lake, the writer found as many as 17 mice per square yard over an area of many acres in extent in the kafir corn field. Computed from the counts made on the measured areas, one arrives at the startling number of 82,280 mice per acre. This gives 2468 pounds of mice per acre, figuring that  $33\frac{1}{3}$  house mice weigh one pound. Really the number of pounds of mice would be greater because 15 of every 100 seen here were meadow mice (*Microtus californicus*), which are much larger animals than house mice (*Mus musculus*). In the middle of the afternoon, here in the western part of the lake basin, most of the meadow mice were in burrows 4 to 12 inches long and extending 4 to 8 inches below the surface. Usually more than one, and sometimes as many as four, animals were found in a single burrow. Most of the house mice were under clods, kafir corn stalks, or any kind of rubbish present. Any such shelter harbored as many house mice as could crowd under it, and the noses and tails of many projected out at the edge of the shelter. As one drove over the field in a car hundreds of mice could be seen, at any given moment, scurrying over the ground, into holes or toward the shelter afforded by clods or bits of rubbish. The ground on this kafir corn field was fairly clean; practically all vegetation, except the butts of the kafir corn stalks, had been eaten by the sheep. Most of these remaining butts were wholly or partly covered by dirt thrown up by the mice, which had worked the soil over to such an extent that it

gave the appearance of having been recently cultivated. It is not to be inferred that 82,280 mice was the average number per acre in the entire lake basin. The average number present when I counted them as well as the original average number just before the migration began, was less. Many of the mice found here probably came from other parts of the lake basin, for on the adjoining bare barley fields only one mouse in every five square yards was found.

Investigation two days later, on January 16, in the opposite (east) end of the lake basin revealed notably fewer mice in both the barley and kafir corn fields than were found in the western part of the basin; one mouse to every 5 square yards in the kafir corn field, and one to every 20 square yards in the barley field, were found in the eastern part.

Mr. George Carlisle, watchman on the levee near this point, reported, on this date, fewer mice about his dwelling than at any time since the second invasion occurred. It thus seems that the majority already had migrated out of this part of the lake basin. The decreased number noted by Mr. Carlisle was a part of the general lull mentioned above. In the invaded oil fields on the west side of the lake, poisoned wheat placed in yards about houses netted, at each house, in the morning, from 15 gallons to as much as 6 ordinary wheelbarrows full of dead house mice. Equal quantities were found at the oil derricks. In one barn on the Honolulu [Oil] Company's property, where grain was stored, approximately two tons of mice, according to reliable report, were killed in one day when the grain was sifted and moved. A series of four furrows surrounded this company's property and in the second furrow back from the lake, where it paralleled the lake margin, an average of between 15 and 16 dead mice per linear foot was found on the third day after the furrow had been made. Others that had taken poisoned grain in the trench went some distance away from it and might be found dead beneath bushes or any other shelter. This trench was about five miles long and it was computed that one-half million mice had been killed by eating the grain placed in it. The trench nearest the lake contained many more dead mice than the second one, and the third and fourth fewer than the second one.

Here in the barren hills, where there was only one xerophytic shrub to about every nine square yards, the house mice, as in other parts of the area, were most active at night, but large numbers were active during the daytime too. Every bush and other plant sheltered several mice. East of the lake, in the farming district, there were

equally as many. Grain bins that I saw had literally thousands swarming about in them; haystacks sheltered nearly as many; and the fields, since they had not been grazed by domestic stock, sheltered millions more. In one grain bin 20 feet square, that was two-thirds full of sacked barley, it was computed that 3520 mice were in sight at one time. These were on the surface of the grain, on rafters, and on the pole plates. Many times this number unquestionably were out of sight in and among the sacks of grain. At night, on the highway that passes along the north side of Buena Vista Lake, the illumination from the headlights of one's car revealed hundreds of live mice at any given instant. From actual counts, it was computed that 17 miles of this highway averaged one dead house mouse to every square yard of pavement. In places, of course, there were dozens of dead mice per square yard. I was reliably informed that the number of dead mice had been much greater on the highway, but that three days previous to my visit, rains washed much of the highway clean. Truly, the number of mice was almost unbelievable, and one who has not seen this or a similar outbreak can scarcely comprehend the vast numbers that can occur in a given area of limited extent. Certainly the numbers were to be reckoned in tens, and possibly in hundreds, of millions.

### ECONOMIC BEARINGS

The plague has economic importance, largely by reason of damage wrought to property by the mice. Actual damage that the mice were seen to do included the destruction of quantities of stored grain; the reduction of large stacks of hay (really straw stacks that here are used for hay) to mere piles of chaff, thus rendering them totally unfit for stock food; the destruction of foodstuffs, clothing, bedding, linen, etc., in houses; and the gnawing of holes through the floors and walls of frame buildings. It seems probable that the mice would damage growing crops although certainly not to the extent that equal numbers of meadow mice (*Microtus*) would.

The house mice constitute a general nuisance on numerous counts. Many of the people have a general horror, on no specific grounds, of such vast hordes of mice. A more tangible objection to them is the condition they cause on the highways. It is a fact that at certain places on the highway so many mice are killed by automobiles that the pavement is made slippery. This comes about in the following way:

When one mouse is killed, as many live ones as can crowd around it, come out and feed on the carcass of the one killed. If struck by a passing car this group may provide ten dead mice for others to feed on, and by numerous repetitions of what has just been described, places, of various extent, on the highway are slushy with dead mice. During the day fewer mice venture out on the highway, and those killed there during the night largely dry up during the day. Thus the stench from decaying mice is not so noticeable as might be expected.

Where large numbers of the mice congregate, as in grain bins and haystacks, the stench arising from the voided body excrements is highly offensive and nauseates many persons. In one observed instance a laborer working at a haystack was so nauseated by the stench from the mice as to vomit severely.

In buildings that are not mouse-proof, persons commonly have their sleep interrupted by the numbers of mice that run about over the bedding. On arising in the morning mice are not infrequently found in one's clothing and shoes. During the day, even, when going about ordinary tasks, mice on occasion enter one's clothing. All these things, together with the actual damage done by the mice, naturally have caused considerable concern among the people living in the infested area.

Although the plague has its serious possibilities, these, in one respect, are minimized to at most half what they would be in a uniformly cultivated country; for unpopulated areas of dry, barren, rolling land extend far north and south of Buena Vista Lake. In this territory there is scarcely anything valued by man, and the present numbers of mice can naturally do no immediate damage. The scarcity, there, of food and cover of the kind required by the house mice probably will prevent them from breeding there, and it seems hardly possible that sufficient numbers will migrate through these areas, and beyond into cultivated country, to become a menace to man. West of Buena Vista Lake, in the thickly populated oil-fields region, there is much property that the mice can continue to damage. Shelter from enemies, safe breeding places, and food can be found in the towns of Taft, Maricopa, and Fellows, and about the houses and equipment in the oil fields; and it appears that a large house-mouse population, although not so large as the one now in the same area, might be present there for a considerable time unless active control measures are employed.



Since this inhabited area immediately west of Buena Vista Lake is isolated by semi-desert, it seems improbable that the house mice would, by migrating out of it, be able to do damage elsewhere. East of Buena Vista Lake the situation has an entirely different aspect, however, for the land there is cultivated and is continuous with the cultivated land that extends many miles to the east and northeast across the San Joaquin Valley. It is not impossible that the migrating mice will find there food and cover permitting them to multiply, and will eventually invade, in large numbers, territory now far distant from the infested area. If not probable this is seemingly possible, and control measures that would stop the spread to the eastward would guarantee protection, from this particular mouse population and its progeny, to all inhabited territory except that now infested.

### BIOLOGICAL INFERENCES

No mice less than three-fourths grown were found. Since it is commonly known, from laboratory experiments, that shortage of food curtails or stops reproduction in mice, the exhaustion of food in the Buena Vista Lake basin is suggested as the probable cause for the apparent absence of young mice among the thousands the writer saw. No evidence of disease of any kind that might be expected to destroy the mice was noted by the writer up to the date of his departure, January 16, 1927. Judging from what has happened during marked increases in the population of other rodents, some epidemic eventually should, of course, be expected to occur here.

Among animals that are subject to such enormous and sudden increases in population, and equally sudden decreases, as are house mice, it may be inferred that natural selection would operate at an accelerated rate. For instance, with the present scarcity of food in the Buena Vista Lake region, it can be understood how certain individual mice that are able to survive longest without sufficient food would live to produce offspring, whereas the millions less fit in this respect would die and leave no progeny. Assuming that this physiological fitness were heritable, a marked change might occur in this respect within a short series of generations. Perhaps the example chosen is not the most happy one; but it suggests one, at least partial, explanation of the apparently unequal rates of evolution of different descent-lines of animals that come to the attention of the palaeont-

ologist. Certain characters would seem more rapidly to be selected for in a kind of animal that is subject to rapid increases and decreases in population than in a kind whose population remains relatively constant through long series of generations.<sup>1</sup>

The radial migration resulted, at first, in apparently equal numbers of the mice moving outward in all directions. Seemingly, therefore, no choice of destination was made by the mice; perhaps more properly speaking, there was no stimulus or positive attraction causing all of, or even the majority of, the mice to move in one given direction rather than in another. Some mechanical factor or factors, then, might seem most likely to be the cause of the movement. At first thought the situation might seem explicable by assuming that the individuals were repellent to one another, as indeed is known to be the case, among individuals of single species, in certain other kinds of mammals and in certain kinds of birds. However, where vast numbers of mice were seen by the writer crowded under a given shelter during the day no dead ones were found; no evidence was forthcoming that they attacked one another or that they otherwise were inter-individually intolerant. If the suggested individual-repellent explanation be considered, one is also led to wonder why, at any given point except the central one, as many mice do not go in one direction, of all the possible ones, as in any other. That they do not is obvious; it is only from the center of the source-area that they tend to move outward in all directions. To assume that the movement of one mouse in a given direction acts as a stimulus for another one near-by to do the same, or that this movement at least discourages the latter from going in a different or exactly opposite direction, explains the movement once it is begun. But of course it could not explain the equal movement in all directions from the one central point; in fact, if such were the determining factor at the beginning of the migration, a radial migration of the type just described would be prevented. Perhaps, then, a mechanical cause starts the migration; after the animals have once gone, for a given length of time, in a certain direction, some sort of impulse is developed to continue. But what the stimulus for guidance may be is not clear.

It also might be that the mice are inter-individually repellent when not migrating, but once they leave their home ranges, each feels as an

<sup>1</sup> After writing the above, the article by Elton, Periodic fluctuations in the numbers of animals; their causes and effects, *British Jour. Exper. Biol.*, 1924, pp. 119-163, has come to hand. In that article the reader can find a fuller treatment of the rôle that fluctuations in population may play in natural selection.

intruder would when he had transgressed into the range of another. Because of this and the fact that none now has 'property rights' to defend, the inter-repellent factor becomes non-operative, although the initial movement might have been caused by this factor by reason of the condition of over-population having restricted the home ranges. Perhaps sufficient reflection on the possible causes will reveal one explanation to be far more probable than any of the others and one which will explain all the known facts; certainly the question is worth study where opportunities for observation present themselves. It is mainly to attract the attention of some future investigator that the matter is mentioned here.

The house mouse is an exotic species that probably has not been in the Buena Vista Lake region longer than fifty years. In the case of other introduced species that multiply rapidly in their new environment, it generally is found, when we cast about, that the natural enemies which hold any one particular species in check in the original home are lacking in the new one. Although the same causes may be operative in the present case, there are, so far as known, normally about as many native organisms of equal effectiveness that prey on the house mouse here as there are in its supposed native home, Asia. It is pertinent to recall that excessive increases in population of native mice have occurred at various places in the world.

According to Hinton (*Rats and Mice as Enemies of Mankind*, British Museum [Nat. Hist.], Economic Series, no. 8, 1918, p. 41) where sudden increases in population of house mice occur over a large area—the main instance cited by Hinton is one that occurred in South Australia and Victoria in 1916 and 1917—native species of mice also increase notably in numbers. The present writer did not find this to be the case at Buena Vista Lake, except as regards one species, the meadow mouse (*Microtus californicus*). White-footed mice (*Peromyscus*) were not more abundant than usual in a locality of this nature; kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus*) were not more abundant, if as abundant, as usual. In fact no *Perognathus* were seen by the writer although they are known to occur in the Buena Vista Lake region. It is possible that, in this region, they hibernate during January. Meadow mice (*Microtus*) were much in evidence, but their slightly greater numbers were more apparent than real, for the destruction of all cover in the lake basin forced the meadow mice out and left them exposed as they would not have been under normal conditions. Such over-abundance of meadow

mice as does exist would constitute, if the house mice were not present, only a potential danger, it is believed, and not an operative destructive agency of much consequence at the present time. The most abundant food was grain. This was more suited to the house mouse than to the meadow mouse whose food predilections, at least in *Microtus californicus*, indicate a partiality for green vegetable food. Perhaps the grain was more suited to the house mouse than to *Peromyscus*, *Perognathus* or *Dipodomys*. If so, this might explain why the numbers of the house mouse, instead of some other, or all other, species of mice in this region increased so notably. Another pertinent fact is that the fecundity of the house mouse is known to be greater than that of the kangaroo rat. Probably, also, the house mouse is better able to withstand the unfavorable conditions arising from irrigation than are the kangaroo rat and pocket mouse and, possibly, the white-footed mouse.

Counts of thousands of mice that had died from eating poisoned grain showed 400 house mice to 1 of all other species combined. This is believed to be a fair estimate of the relative numbers present between January 12 and 17. Relatively more meadow mice were present in the lake basin and outside the lake near its margin, but relatively fewer farther away from the lake. The house mice were migrating more rapidly than the meadow mice, and at any date later than the period of investigation here reported on, relatively more meadow mice will be found where the two species occur together, and the relative number of meadow mice will appear to be greater than was actually the case at the beginning of the outbreak. No evidence of migration of the other kinds of mice noted, *Peromyscus* and *Dipodomys*, was seen. In fact, evidence furnished by the individuals found dead in places where concentric, circular furrows had been plowed and treated with poisoned grain indicated that there was no migration by these genera.

Hawks, owls, and ravens were more abundant here than usual. This statement is made both on the basis of reports of local residents and on the writer's own personal field observations here as compared with those in similar localities where mice were not overly abundant. Named in order of their abundance from first to last, the hawks noted were: Marsh Hawk (*Circus hudsonius*), Western Red-tailed Hawk (*Buteo borealis calurus*), Desert Sparrow Hawk (*Falco sparverius phalaena*), and a rough-legged hawk (*Archibuteo*, sp.?). Barn Owls (*Tyto pratincola*) were abundant, and Short-eared Owls (*Asio flammeus*) were seen wherever there was terrestrial cover, a condition that

obtained only at the eastern end of the lake. Here, where there were scattering trees, the hawks were more abundant too. On the northern, western, and southern sides of the lake the country is barren, and few hawks or owls were noted. Western Red-tailed Hawks sitting on the bare ground and Barn Owls about buildings were the only raptores noted there. Ravens (*Corvus corax sinuatus*) were present in flocks of 15 to 40 and fed on the mice. They preferred the meadow mice and ground squirrels to the house mice, probably because of the larger size of the first mentioned two. One Raven, that had died apparently from eating poisoned mice, was seen. Piles of mouse-remains, representing dozens of individuals, were noted about the bases of several fence posts where Ravens had carried the animals to feed on them. Pellets of hawks and owls found were composed entirely of remains of mice, largely house mice but some meadow mice.

It was discouraging to note the lack of appreciation displayed by the local residents, of the beneficent rôle played by the carnivorous birds. One man told me that he had "been troubled more lately with those darned monkey-faced owls [Barn Owls] than for several years" and had recently "shot seven that insisted on hanging around the place." Several dead Western Red-tailed Hawks were seen hanging on fences where they had been placed by hunters.

Although predatory birds were abundant, predatory mammals were extremely rare in the infested area. In fact I saw none, nor even any sign, such as tracks, droppings, and inhabited burrows. In similar territory where normal numbers of coyotes, kit foxes, striped skunks, spotted skunks, badgers, and weasels occur, one would, in doing the same amount of field work that I did here, see signs of the animals on numerous occasions and probably some of the animals themselves. Reports of residents of the region when questioned on this point, were without exception to the effect that the above mentioned mammals used to be frequently noted, but not recently. When questioned as to the length of time this scarcity had been evident, the replies usually were: "I haven't seen any for two years." Sometimes the time was given as "about a year and a half." As to the cause of this scarcity of predatory mammals, the people questioned ascribed it to the fact that the animals mentioned had to have water and consequently left after the lake had been dry for a while, or to unknown causes. As a matter of fact water was available in sloughs and irrigation ditches and the drying up of the lake would not account for the disappearance of all carnivores.

Naturally puzzled at this apparent absence of these predatory enemies of the mice, the writer kept careful watch for any evidence of them, but no carnivorous mammal, or sign of any, was found. Subsequently it was learned that an intensive campaign against the coyotes of the region had been waged under the auspices of a federal bureau in the winter of 1924-25,<sup>2</sup> at the request of, or at least for the assumed benefit of, sheepmen since the coyotes and bobcats take toll of the flocks at certain seasons. The campaign was carried on by generously distributing poisoned baits over the country. Known results of the campaign are indicated by the following sample observation made shortly after the time it was being carried on. "For instance, near Buena Vista Lake [I am assured that this was within two miles of the lake], in January, 1925, in a distance of one mile along a road, 5 skunks and 2 coyotes were found dead. In this locality, 25 skunks, 8 coyotes and 7 kit foxes were found dead by Arthur Oliver, the evidence being conclusive that they had been killed by poison set out for coyotes. In general it was found that the poison campaign was terribly effective; perhaps more so to kit foxes and skunks than to coyotes" (field notebook in Museum of Vertebrate Zoology).

Now it is of course known that several factors beside the natural enemies of mice determine their numbers; e.g., favorable climate, and other factors that foster abundant plant growth, thus providing necessary food and shelter. Here in the Buena Vista Lake region the climate is mild, and it would not appear to be directly so important in controlling the numbers of mice as in some other places. Flooding by irrigation, however, comes under this head. In any place, climate would not be so effective in removing the surplus of mice as it would the surplus of certain other species. The essential reason for this is well stated by Hinton (*loc. cit.*, p. 45), as follows: "Despite the heavy toll levied by accident and competition, free-living creatures, like small birds, usually have a large surplus at the end of summer; and that surplus must be removed [largely] by the severe weather of the following seasons. On the other hand, more or less earth-bound animals, like the Muridae [to which family the house mouse belongs], with their habits of constructing warm nests in dry burrows and of amassing stores of provisions, are enabled to withstand all but the most severe weather. In their case the surplus must be removed chiefly by accidents and competition. Their habits render small

<sup>2</sup> Monthly Bulletin of the Department of Agriculture, State of California, XIII, July-December, 1924, pp. 165-67.

rodents the easiest of prey; in fact, they form the staple food of every one of our carnivorous mammals,<sup>3</sup> with the exception of the Otter."

It may also be pointed out that in the normal, or usual state of population of animals,<sup>4</sup> one given carnivore feeds on several species of prey; but when for any reason one species of prey becomes more numerous than the others, then the carnivore naturally, because of the ease and readiness with which the prey can be secured, concentrates upon that one. There is, then, a certain optimum point of population-size for a species (which condition, I suspect, is capable of accurate determination) that calls forth the maximum effectiveness of the other animals that prey upon it. When the usual relative numbers of all the different species, both carnivores and herbivores, are present, this optimum point seldom is passed or even reached, and the condition of an over-population is thus prevented by the animals that play the carnivorous rôle. It is known that house mice attain sexual maturity by the time they are three months old at most and that, on the average, under favorable circumstances they produce a litter at least once each month. The litters average from five to six. In two years' time, then, breeding at this rate and assuming that all the mice lived to reproduce their kind, two adult mice producing a litter at the end of the first month, have a potentiality of 3,701,257.

Let us suppose, for the sake of illustration, and not for the sake of assuming that the number selected is correct as to the actual number produced by one pair here, that at Buena Vista Lake one pair of house mice was responsible for one one-thousandth of this number, that is, 3701. Four pairs of mice then would, at the end of two years, be responsible for 14,804 mice. If, however, predatory mammals, or anything else, should destroy at the beginning, half these 8 mice, involving 2 females, the number at the end of two years would be only half of 14,804, or 7402. It therefore is readily seen that the absence at the *present* time, of natural checks, is not the important factor, but that their absence when the increase in population *began* was the important factor that might have prevented or at least greatly decreased the eventual outbreak. Although suitable shelter was abundant for the mice, it was not of the kind that would have been

---

<sup>3</sup> This statement is made with regard to the carnivorous mammals in the British Isles but, with the exception of the Mountain Lion and Skunks, it also applies in California.

<sup>4</sup> This statement does not imply a static population but rather one that fluctuates within restricted limits. It seems well established that, within the temperate regions, where relatively more species of mammals occur in a given area, fluctuations in population are not so great as in more northern latitudes.

impregnable to the enemies of the mice. Although food was abundant, no evidence is forthcoming that it was more abundant than in similar fields elsewhere at times when the weather conditions were essentially as they were in the past two years at Buena Vista Lake. As Hinton (*loc. cit.*, p. 46) has said, "The weather may be lenient to rodents, the carnivora never." At Buena Vista Lake the carnivores had been eliminated.

The causes of this over-abundance of population of house mice may therefore be stated as: favorable meteorological conditions, abundant food and shelter, and removal of the principal natural enemies of small rodents that normally hold their numbers in check. The factor determining the time of the spectacular emigration of the mice was, probably, the destruction of their food and shelter.

Unfavorable meteorological conditions alone, a lesser amount of food and shelter alone, would have, and the presence of the normal number of carnivorous mammals alone might have, prevented the excessive increase in numbers.

A point of general interest, as well as one having a direct relation to the present subject, is that the cost of the campaign carried on against predatory mammals in the Buena Vista Lake region, together with the actual loss resulting from the destruction of fur-bearing mammals, is believed by some persons to have been far more than the loss previously sustained by stockmen from attacks of predatory mammals upon their flocks. Now the plague of house mice follows, and in so far as this plague is due to the destruction of the natural enemies of the mice, the predatory mammals, a proportional amount of the large monetary damage done by the mice and the sums spent in attempting to control them, is to be added to the already over-balanced debit side of the ledger. One conclusion seemingly proper to draw from this is that due caution should be exercised in meeting the demands of any one minority group of persons. Lack of this caution may result, as it seemingly has in the instance just cited, in heavy loss to the community at large.

*Transmitted January 31, 1927.*





THE MUSCULAR ANATOMY OF THE  
AMERICAN BADGER (TAXIDEA TAXUS)

BY  
F. RAYMOND HALL

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 8, pp. 205-219, 2 figures in text

Issued July 28, 1927

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA



CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# THE MUSCULAR ANATOMY OF THE AMERICAN BADGER (*TAXIDEA TAXUS*)

BY

E. RAYMOND HALL

(Contribution from the University of California Museum of Vertebrate Zoology)

---

## INTRODUCTION

Since material, in the flesh, representing the family Mustelidae has been received at the Museum of Vertebrate Zoology, the writer has taken the opportunity to dissect representatives of several genera and has made notes on their anatomy in the belief that, eventually, accumulated observations will indicate relationships that are not now apparent. So far as is known, no description of the musculature of the American Badger (*Taxidea taxus*) has ever been published.

To avoid repetition in description, those muscles that agree with the descriptions given of the corresponding muscles of *Mephitis* or *Martes* (see Hall, The muscular anatomy of three mustelid mammals, *Mephitis*, *Spilogale*, and *Martes* [Univ. Calif. Publ. Zool., vol. 30, pp. 7-38, 1926]) are merely stated to be as in one or other of these genera. No account is here given of the facial and skin muscles, a description of which is reserved for treatment in another connection. The order of arrangement is that employed by Hall (*op. cit.*).

The material dissected consists of one adult male *Taxidea taxus* subsp.; now preserved as no. 37282, Mus. Vert. Zool.; skin and complete skeleton; obtained at Millett Post Office, Nye County, Nevada, by Miss Annie M. Alexander.

## DESCRIPTION OF MUSCLES

**Digastricus.**—ORIGIN: Anterior face of paroccipital process and ventral face of mastoid bone. INSERTION: Ventral face of mandible from point directly below  $M_2$  posteriorly to point directly below inferior mental foramen.

**Masseter, temporalis, pterygoideus, thyreohyoideus, and geniohyoideus.**—As in *Mephitis*.

**Mylohyoideus.**—ORIGIN: Median alveolar border of each mandible from symphysis to inferior dental foramen. INSERTION: Anteriorly (from symphysis to point opposite  $M_2$ ) into fascia extending over the geniohyoideus and posteriorly (from point opposite  $M_2$  to point 15 mm. posterior to same) into median raphe. REMARKS: This muscle, as compared with the corresponding ones in *Mephitis* and *Martes*, is weak.

**Hyoglossus, styloglossus and genioglossus.**—As in *Mephitis*.

**Spinotrapezius.**—ORIGIN: Neural spines of thoracic vertebrae, 1–10. INSERTION: Vertebral end of scapular spine for distance of 15 mm. REMARKS: As in *Martes*.

**Acromiotrapezius.**—ORIGIN: By fascia from mid-dorsal line, from occiput to point opposite scapular spine (100 mm. posterior to occiput) and from fascia, common to muscles of two sides, extending 30 mm. farther posteriorly. INSERTION: Spine of scapula between points 24 mm. and 55 mm. distant from vertebral border; thus between areas of insertion of spinotrapezius and omotrachelian. REMARKS: The anteriormost fibers reach the lambdoidal crest at the median line and for a distance of 50 mm. posterior to this point the fascia connecting the muscle to the mid-dorsal line is only 2 to 4 mm. long, but posterior to this the fascia becomes more extensive and the muscle fibers terminate 30 mm. short of the mid-dorsal line at a point as far posteriorly as the scapular spine. The anterior 50 mm. is overlapped by the clavodeltoideus.

**Clavotrapezius.**—ORIGIN: By thin tendon from mid-dorsal line, from lambdoidal crest to point 50 mm. posterior to same and on lambdoidal crest laterally (40 mm.) to horizontal line touching dorsal margin of foramen magnum. INSERTION: Tendinous line at anterior end of clavodeltoideus. REMARKS: There is no clavicle and only a thin tendinous line separates the clavodeltoideus from the clavotrapezius and cleidomastoideus. The clavotrapezius overlaps the acromiotrapezius on the mid-dorsal line for a distance of 50 mm. On the lambdoidal crest the thin tendon of the clavotrapezius extends up to that of the sternomastoideus (not shown in fig. 1) and the adjacent margins of these two muscles are in contact with one another for a distance of 90 mm. posteriorly, which is 20 mm. anterior to the tendinous line marking the position that the clavicle occupies in many other forms. Thus, the spinotrapezius overlaps (covers in ventral view) the cleidomastoideus.

**Rhomboideus cervicis.**—ORIGIN: Spines of first 4 thoracic vertebrae and mid-dorsal line of neck up to head. INSERTION: Vertebral border of scapula from anteriormost extension of triangular surface at vertebral end of spine to inferior angle of scapula. .

**Rhomboideus capitis.**—ORIGIN: Lambdoidal crest, from sagittal crest to horizontal line touching dorsal margin of external auditory meatus. INSERTION: Root of scapular spine at posterodorsal margin of supraspinatus fossa. REMARKS: The medial border of this muscle lies against the lateral border of the rhomboideus cervicis, and the two muscles, although quite distinct from one another, form a broad sheet on the dorsal side of the neck.

**Rhomboideus profundus.**—ORIGIN: Tendinous fascia on latero-ventral face of complexus. INSERTION: Root of scapular spine by flat tendon that spreads out widely over the posterodorsal part of the supraspinatus muscle.

**Cleidomastoideus and omotrachelian (levator claviculae ventralis).**—As in *Mephitis*.

**Latissimus dorsi.**—ORIGIN: By fascia from tips of neural spines of 5th to 14th thoracic vertebrae, from fascia that extends over lumbar region, and by fibers directly from 11th, 12th, and 13th ribs. INSERTION: In two parts. Ventral fibers with part *C* of pectoralis on antero-internal face of humerus. Dorsal fibers converge and insert with teres major.

**Levator anguli scapulae and serratus magnus.**—ORIGIN: Transverse processes of last 5 cervical vertebrae, rib-cartilages of first 5 ribs, and 7th and 8th ribs proper. INSERTION: Entire vertebral border of scapula and posterior 11 mm. of suprascapular fossa.

**Longissimus dorsi.**—Anterior to the 8th thoracic vertebra this is a well defined muscle which inserts as far anteriorly as the transverse process of the 4th cervical vertebra. The longus atlantis is represented by fibers taking origin as far posteriorly as the 7th cervical vertebra. The fibers insert on the transverse process of the atlas.

**Longus capitis.**—ORIGIN: Transverse processes of cervical vertebrae, 2-6. INSERTION: Ventral face of basioccipital.

**Iliocostalis.**—ORIGIN: Ribs, 13-5. INSERTION: Ribs, 9-1. REMARKS: This is a distinct muscle confined to the thoracic region. The fibers insert on the 4th to 5th rib anterior to the one on which they take origin.

**Spinalis dorsi.**—This muscle becomes differentiated from the *logissimus dorsi* at the 8th rib. It extends forward to the first thoracic vertebra, and a small lateral slip inserts by a long, thin tendon on the 3rd cervical vertebra.

**Interspinales and intertransversarii.**—These muscles have the usual arrangement. Some fibers, however, pass over more than one vertebra between the origins and insertions.

**Splenius.**—ORIGIN: Cervical ligament, from first thoracic vertebra anteriorly to within 50 mm. of lambdoidal crest, and by fascia that extends posteriorly from first thoracic vertebra to fourth thoracic vertebra. INSERTION: By thin tendon on lambdoidal crest, mesially to within 21 mm. of sagittal crest.

**Longissimus capitis.**—ORIGIN: Transverse processes of first 5 cervical vertebrae. INSERTION: By round tendon on mastoid process.

**Complexus tertius.**—ORIGIN: Articular processes of last 6 cervical vertebrae. INSERTION: Posterior face of transverse process of atlas.

**Biventer cervicis major and complexus.**—There is but a faint line indicating separation of these muscles. This line is most pronounced anteriorly at the insertions of the muscles. ORIGIN: Articular processes of first 7 thoracic and last 5 cervical vertebrae. INSERTION: Approximately middle half of lambdoidal crest. REMARKS: The medial border of the *biventer cervicis major* lies against the lateral border of the *biventer cervicis minor* throughout the extent of the latter. The term *major* is added here as a matter of consistency since the term *minor* is employed for the next mentioned muscle.

**Biventer cervicis minor.**—ORIGIN: Cervical ligament from posterior end of sagittal crest to point 50 mm. behind same. INSERTION: Supraoccipital bone between lambdoidal ridge and area of insertion of *rectus capitis* muscles. The area of insertion extends 11 mm. laterally from the median line. REMARKS: The muscles of the two sides exactly fill the triangular space between the two *biventer cervicis major* muscles. The muscle is innervated by branches of the second and third and possibly first cervical nerves, which branches innervate the *biventer cervicis major*. The *rectus capitis posterior* muscles are innervated by other branches of the cervical nerves. The *splenius*, also, is innervated by branches of the cervical nerves distinct from those which innervate the *biventer cervicis major* and *minor*. Thus, such evidence as is furnished by the innervation indicates this muscle to be a derivative of the *biventer cervicis major*. The lack of any

connection with the spine of the atlas, the place of insertion (on a line with the areas of insertion of the biventer cervicis and splenius), and the evidence from the innervation, seemingly preclude a derivation from the ventrally adjacent rectus capitis posterior major. There is also a triangular space at the back of the skull between the two splenius muscles. The manner of origin of the biventer cervicis minor, from the cervical ligament, is similar to that of the splenius, and the origin is continuous anteriorly from the point where that of the splenius leaves off. However, the fibers of the splenius extend more laterally than those of the biventer cervicis minor; thus the two biventer cervicis minor muscles do not quite fill the triangular space between the two splenius muscles. To summarize: This muscle seemingly was derived from the splenius or from the biventer cervicis. Derivation from the splenius is indicated by a similar origin. Derivation from the biventer cervicis is indicated by a common innervation. In the present case the writer places more reliance on the innervation and accordingly designates the muscle as biventer cervicis minor.

**Rectus capitis posterior major.**—ORIGIN: Caudal third of spine of axis. INSERTION: Occiput immediately dorsal to area of insertion of rectus capitis posterior medius.

**Rectus capitis posterior medius.**—As in *Martes*.

**Rectus capitis posterior minor.**—ORIGIN and INSERTION: As in *Mephitis*. REMARKS: This muscle is as large as the rectus capitis posterior medius. The rectus capitis posterior major is the largest of the three.

**Obliquus inferior and obliquus capitis superior.**—As in *Mephitis* except that the area of insertion of latter muscle is confined to posterior face of mastoid bone.

**Extensor caudae medialis, extensor caudae lateralis, and adductor caudae externus.**—As in *Mephitis* except that the last muscle is divided into two parts, the medial one of which extends farther posteriorly than the lateral one.

**Adductor caudae internus.**—ORIGIN: Medial face of innominate bone, on spine of ischium just medial to posterior border of acetabulum. INSERTION: Transverse processes of caudal vertebrae, 2-5. REMARKS: A weak muscle.

**Iliocaudalis.**—If present, fused with levator ani.

**Flexor caudae longus, flexor caudae brevis, iliopsoas, and quadratus lumborum.**—First two as in *Martes* and last two as in *Mephitis*.



**Psoas minor.**—ORIGIN: Last 4 lumbar vertebrae. INSERTION: As in *Mephitis*.

**Sternomastoideus.**—ORIGIN: Cephalic end of manubrium anterior to first costal tubercle. INSERTION and REMARKS: The muscle of one side is fused with its opposite for a distance of 45 mm. anterior to

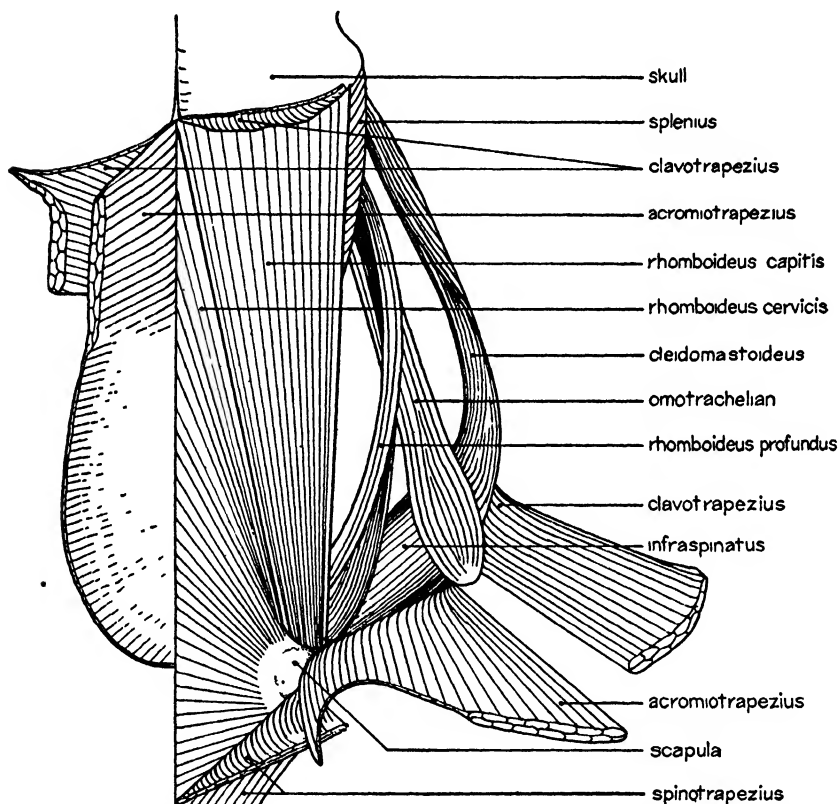


Fig. 1. *Taxidea taxus*,  $\frac{1}{2}$  natural size. Slightly diagrammatic view of muscles seen on dorsal side of right half of neck after removal of platysma. The spinotrapezius and clavodeltoideus are shown as cut and laid back, thus exposing the deeper muscles.

the origin. The muscle on each side consists of a deep and a superficial part. The superficial part is a flat band 11 mm. wide that inserts by a thin, flat tendon on the lambdoidal ridge from the lower margin of the line of origin of the clavotrapezius to a point situated on a horizontal line passing through the middle of the external auditory meatus. This superficial part lies on the lateral half of the deep part and, except in the posterior 45 mm., it is in contact laterally with the medial margin of the clavodeltoideus. The deeper portion is 27 mm. wide and inserts by a round tendon on the mastoid process. This

deep part, except near its origin and insertion, is divided into a laterodorsal and medioventral part.

**Sternohyoideus.**—As in *Mephitis* except that it is 9 mm. wide and present on left side only.

**Sternothyreoideus.**—As in *Mephitis* except that muscle of right side is heavier than its opposite and that the two muscles arise inside the thoracic cavity from the second and third (not the first) costal cartilages.

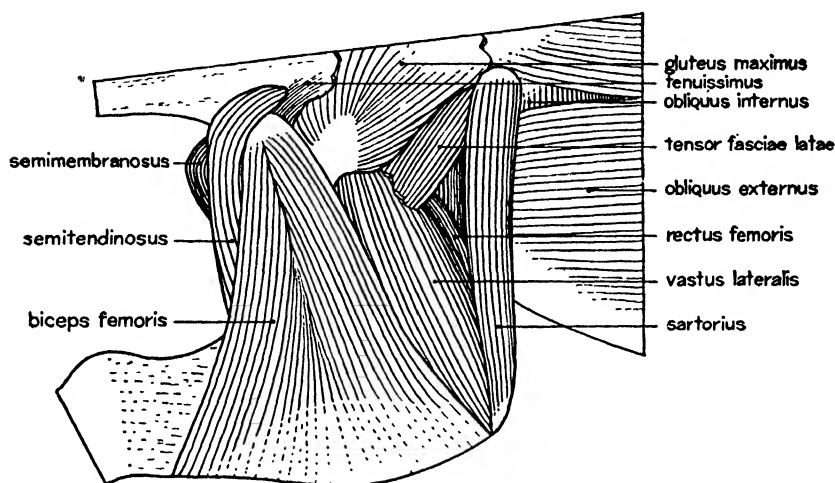


Fig. 2. *Tuxidea taxus*,  $\frac{1}{2}$  natural size. Muscles seen on lateral side of right hind leg after removal of panniculus carnosus and fascia lata.

**Scalenus longus.**—ORIGIN: Transverse processes of cervical vertebrae (see REMARKS). INSERTION: In 3 parts. Part *A*, on first rib just below its head. Part *B*, ribs 3–4. Part *C*, ribs 4–5. REMARKS: Part *A* consists of fibers that arise from the transverse process of the atlas. A small bundle of these fibers inserts on the transverse process of the third cervical vertebra but the larger mass of fibers, taking origin from the atlas, inserts on the first rib. Parts *B* and *C* take origin from the transverse processes of the 2d, 3d, and 4th cervical vertebrae.

**Scalenus brevis.**—ORIGIN: Transverse processes of last 5 cervical vertebrae. INSERTION: First rib. REMARKS: This is distinct from the scalenus longus. The brachial plexus lies ventral to all the scalenus muscles.

**Rectus capitis anterior.**—ORIGIN: Ventral face of inferior arch of atlas and ventral face of transverse process of atlas. INSERTION: Distinct fossa on lateral part of basioccipital, adjacent to tympanic bulla, between carotid canal and foramen lacerum posterior.

**Rectus capitis lateralis and longus colli.**—As in *Mephitis* except that latter muscle extends to anterior end of 7th thoracic vertebra on which a few fibers insert.

**Pectoralis.**—*Note on the humerus:* To facilitate description of the attachments of certain muscles, a restricted meaning has been applied to the term deltoid ridge. The humerus of *Taxidea* is highly modified in accordance with the animal's fossorial mode of life. In this paper the term deltoid ridge denotes the strong ridge which begins on the posterolateral side of the greater tuberosity and that extends distally and medially to a point near the middle of the anterior face of the humerus. At this point the deltoid ridge meets a strong ridge, that will be called the pectoral ridge, which extends down the anterior face of the humerus from a point 5 mm. medial to, and 8 mm. ventral to, the greater tuberosity, to a point 5 mm. lateral to, and 6 mm. proximal to, the supracondyloid foramen. Thus, in the specimen before me the pectoral ridge is 67 mm. long. The part below the union of the deltoid and pectoral ridges will be spoken of as the distal half of the pectoral ridge and the other part as the proximal half. The term supracondyloid ridge refers to the strong ridge, or crest, developed above the external condyle. **ORIGIN:** Three clearly defined parts of the pectoralis are present. Part *A* (this corresponds to *A* and *B* of *Mephitis* and *Martes*) arises from the entire longitudinal extent of the sternum and inserts on the whole length of the pectoral ridge. The distal half of this insertion is tendinous. Part *C* (*B* is included in *A*) arises from the middle 40 mm. of the sternum and inserts on the entire proximal half of the pectoral ridge. Part *D*: At the origin there are two parts, a small round one coming from the cephalic end of the manubrium, anterior to the first costal tubercle, and a second part, deep to *A* and *C*, coming from the sternum between the first costal tubercle and a point 30 mm. posterior to same. These insert together by a flat tendon on the anterior face of the greater trochanter.

**Serratus posterior superior.**—**ORIGIN:** Ribs, 3–11. **INSERTION:** Fascia covering longissimus dorsi. **REMARKS:** The fibers extend antero-dorsally and the slips unite to form one muscle.

**Serratus posterior inferior.**—As in *Martes*.

**Transversus costarum.**—**ORIGIN:** By tendinous sheet between ribs 3–5. **INSERTION:** By fleshy fibers on first rib.

**Levatores costarum, intercostales externi, intercostales interni, transversus thoracis, and diaphragma.**—As in *Mephitis* except that transversus thoracis consists of 8 bands.

**Obliquus abdominis externus.**—ORIGIN: By 11 separate slips from ribs 4–14, and by fascia from lumbar region for a distance of 15 mm. posterior to 14th rib. INSERTION: As in *Mephitis*.

**Obliquus abdominis internus.**—ORIGIN: Lumbodorsal fascia and crural ligament. INSERTION: Anterior fibers on 14th rib (there is a rudimentary 15th rib). Other fibers on midventral line as in *Mephitis*.

**Transversus abdominis.**—As in *Mephitis* except that aponeurosis measures 20 mm. instead of 9 mm. in width.

**Rectus abdominis, spinodeltoideus, and acromiodeltoideus.**—As in *Mephitis* except that rectus abdominis inserts also on lateral face of second costal cartilage.

**Clavodeltoideus.**—ORIGIN: Tendinous intersection between this muscle and the clavotrapezius and cleidomastoideus. INSERTION: Distal half of pectoral ridge.

**Supraspinatus, infraspinatus, teres minor, and subscapularis.**—As in *Mephitis*.

**Teres major.**—ORIGIN: Axillary border of scapula from inferior angle to inferior spine which is well developed in *Taxidea*. INSERTION: By flat tendon, common to this muscle and part of latissimus dorsi, 12 mm. wide on medial margin of pectoral ridge, beginning at point 27 mm. below top of greater tuberosity.

**Epitrochlearis and biceps brachii.**—As in *Martes* except that the two parts of the epitrochlearis are of equal length and width.

**Brachialis.**—ORIGIN: Posterior and lateral faces of humerus, vertically from inferior margin of head to proximal end of supracondyloid ridge, and transversely from the deltoid crest to a nearly straight line connecting the inferiormost point of the lower margin of the head of the humerus to the proximal end of the supracondyloid ridge. A second part takes origin from the anterior face of the condyloid ridge, medial to the area of origin of the extensor carpi radialis. INSERTION: As in *Mephitis*.

**Triceps brachii.**—In four parts. Caput laterale. ORIGIN: Proximal part of deltoid ridge and inferior margin of greater trochanter and head on lateral side of humerus. INSERTION and REMARKS: As in *Mephitis*. Caput longum as in *Martes* except that origin is from anterior 38 per cent of axillary border of scapula. Caput mediale as in *Mephitis* except that long head takes origin as far as 28 mm. distally from inferior margin of head of humerus. The distal 70 per cent is fused with the caput laterale; and the short head inserts on the

proximal one-half of the posteromedial (toward body) face of the median epicondyle. Caput angulare as in *Mephitis*.

**Anconeus.**—ORIGIN: Entire vertical extent of lateral margin of lateral epicondyle and supracondyloid ridge, and a triangular area on posterior side of distal end of humerus. INSERTION: As in *Mephitis*.

**Brachioradialis, extensor carpi radialis longus, and extensor digitorum communis.**—As in *Mephitis* except that the tendon of the extensor carpi radialis longus that inserts on the third metacarpal is only one and one-half times as wide as the one inserting on the second metacarpal.

**Extensor digitorum lateralis and extensor carpi ulnaris.**—As in *Mephitis* except that the first mentioned muscle is divided. The part going to the 3d and 4th digits takes origin by a long, narrow, flat tendon. The part inserting on the 5th digit is fleshy to the origin and its tendon of insertion is heavier than the tendons inserting on the 3d and 4th digits.

**Extensor indicis and supinator.**—As in *Martes* except that supinator inserts on the proximal 79 per cent of that part of the ulna anterior to the anterior (distal) margin of the semilunar notch.

**Extensor pollicis brevis.**—ORIGIN: Lateral face of proximal 57 per cent of radius and anterior face of ulna from distal end of semilunar notch to within 20 mm. of distal end of ulna. INSERTION: As in *Mephitis*.

**Pronator teres and flexor carpi radialis.**—As in *Mephitis* except that the insertion of the pronator teres is on exactly the distal half of that part of the radius which lies between the head and the proximal end of the styloid process.

**Palmaris longus.**—In two parts. Part *A*, as in *Martes*. Part *B*. ORIGIN: Lateral to and in common with (but not from) part *A*. INSERTION and REMARKS: This is a distinct muscle of about one-tenth the mass of part *A*. It inserts by a short, flat tendon into a fibrous pad overlying (in palmar view) the pisiform bone and ulnar half of the wrist. This fibrous pad has a distinct muscle in it (to which muscle the tendon of part *B* is attached) attaching to the palmar surface of the common tendon of part *A* of the palmaris longus and to the vaginal sheath of the fifth metacarpal. This fibrous pad and contained muscle lie on the palmar surface of the hand and mostly anterior to the flexor digitorum manus brevis.

**Flexor carpi ulnaris.**—In two parts that are distinct from one another throughout. Part *A* takes origin from the ventral (posterior)

face of the olecranon and inserts by a flat tendon, 25 mm. long, on the palmar end of the pisiform bone. Part *B* has the same insertion except that it is not tendinous. It takes origin by a flat tendon, 20 mm. long, from the internal condyle of the humerus. Reexamination of *Mephitis* and *Martes* shows a wholly distinct, second part in *Martes*. This has the same origin and insertion as part *B* of *Taxidea* but is not tendinous at either the origin or insertion.

**Flexor digitorum sublimis.**—ORIGIN: First and second (*B* and *C* of *Mephitis*) heads of flexor digitorum profundus. INSERTION: As in *Mephitis*.

**Flexor digitorum profundus.**—By five heads which unite as in *Martes*. Part *A* as in *Mephitis* except that area of origin extends from posterior (proximal) end of olecranon to within 20 mm. of styloid process. Parts *B*, *C*, and *D* as in *Mephitis* except that each part is distinct. Part *E* takes origin over all but the proximal 8 mm. of the proximal 71 per cent of ventral face of radius. INSERTION: The five tendons insert as in *Martes* but there are no accessory tendons.

**Pronator quadratus.**—ORIGIN: Distal third (disregarding styloid process) of flexor face of ulna. INSERTION: Distal half (disregarding styloid process) of flexor face of radius.

**Flexor digitorum manus brevis.**—This is a strong muscle attaching to the tendon of part *A* of the palmaris longus and to the transverse ligament of the wrist. It inserts into the vaginal sheath of the first digit at the base of the first phalanx. The muscle lies on the palmar surface of the hand ventral to all the other muscles and tendons of the hand except the tendon of part *B* of the palmaris longus.

**Lumbricales.**—As in *Mephitis*.

**Adductor pollicis brevis.**—ORIGIN: Transverse ligament of wrist at middle of wrist. INSERTION: By fibers on palmar surface of base of first phalanx of first digit.

**Flexor pollicis brevis, adductor pollicis, interossei, adductor digiti secundi, adductor digiti quinti, flexor digiti quinti brevis, and opponens digiti quinti.**—As in *Mephitis*.

**Sphincter ani internus.**—As in *Mephitis* except that the muscles are smaller, as are the anal glands which the muscles surround.

**Cau道analis and caudocavernosus.**—ORIGINS: Ventral face of 4th caudal vertebra. INSERTIONS: Both muscles into fascia that is attached to the base of the corpus cavernosum and to Cowper's glands. REMARKS: The two muscles are distinct from one another in *Taxidea*.

**Sphincter ani externus.**—Distinct and in usual position encircling anal orifice. If fibers extended to the testes or to the tail they had been destroyed.

**Caudorectalis.**—ORIGIN: Ventral faces of 6th and 7th caudal vertebrae. INSERTION: Dorsal and lateral faces of rectum. REMARKS: A second muscle whose fibers extend at right angles to those of the caudorectalis (thus transversely encircling the rectum) and which is internal to the caudorectalis, was noted.

**Compressor urethrae membranaceae.**—A heavy muscle whose fibers encircle the urethra transversely as in *Mephitis*.

**Levator ani.**—ORIGIN: Symphysis of ischium, pubis along entire ventral border of obturator foramen just ventral to area of origin of obturator internus and medial face of innominate bone just opposite acetabulum. INSERTION: Ventral faces of 5th and 6th caudal vertebrae.

**Ischiocavernosus.**—ORIGIN: Ventral half of caudal border of posterior ramus of ischium. INSERTION: Bulb of corpus cavernosum penis.

**Retractor urethrae.**—ORIGIN: Medial face of ischium just anterior to, and parallel with, area of origin of ischiocavernosus. INSERTION: Dorsal part of tendinous fascia connecting urethra to posterior end of symphysis and to corpus cavernosum. REMARKS: The muscle is distinct from any other. It pulls the urethra posteriorly. Its main function may be one concerned with the penis, but the muscle's action seemingly would move the urethra through a greater distance than it would the corpus cavernosum. It is possible that the muscle's action moves the distal (anterior) end of the penis ventrally. The name here coined for the muscle suggests its action on the urethra.

**Tensor fasciae latae.**—ORIGIN: By thin, slender tendon from anteroventral angle of crest of ilium. INSERTION: Into fasciae latae. REMARKS: The posterodorsal margin is fused with the anteroventral margin of the gluteus maximus.

**Gluteus maximus.**—ORIGIN: By thin tendon from ilial crest, from fascia covering gluteus medius, and from fascia covering spinalis muscles. INSERTION: As in *Mephitis*.

**Gluteus medius.**—As in *Mephitis* except that the posterior margin is fused with the anterior margin of the piriformis.

**Piriformis.**—ORIGIN: Ventral face of last (3d) sacral vertebra. INSERTION: In common with gluteus medius on proximal end of greater trochanter.

**Gemellus superior, gemellus inferior, iliocapsularis, and gluteus minimus.**—As in *Mephitis* except that origin of gluteus minimus is from slightly more than the posterior half of the ventral margin of the ilium; that is, from the eminence for origin of the rectus femoris to a point 23 mm. anterior to same.

**Quadratus femoris.**—ORIGIN: Dorsal third of lateral side of posterior ramus of ischium. INSERTION: By fibers on posterior face of femur just distal to trochanteric fossa over an area 8 mm. in diameter.

**Obturator externus, obturator internus, and biceps femoris.**—As in *Mephitis* except that insertion of biceps femoris is on proximal 86 per cent of lower leg.

**Tenuissimus.**—ORIGIN: By thin, flat tendon on the broad sheet of tendinous fascia that extends from the spinous processes of the sacral vertebrae to the ischial tuberosity. INSERTION: As in *Mephitis*. REMARKS: The muscle is 9 mm. wide.

**Semitendinosus.**—ORIGIN: Ischial tuberosity. INSERTION: By flat tendon on medial side of cnemial crest, on middle half of tibia.

**Semimembranosus.**—As in *Mephitis*.

**Sartorius.**—ORIGIN: Crest of ilium and anterior half of ventral margin of ilium. INSERTION: As in *Mephitis*. REMARKS: The insertion extends distally over the proximal third of the tibia, on the anterior crest. The muscle is single.

**Gracilis.**—ORIGIN: By flat tendon from ischial symphysis and ventral 20 mm. of posterior ramus of ischium. INSERTION: By thin, short (2 mm.), flat tendon, 8 mm. wide, on medial side of anterior crest of tibia immediately posterior (not distal) to distal 8 mm. of area of insertion of sartorius.

**Adductor femoris and pectineus.**—As in *Mephitis* except that the area of insertion of the adductor femoris extends slightly farther distally.

**Rectus femoris and vastus lateralis.**—As in *Mephitis* except that the area of origin of vastus lateralis begins at a point 35 per cent of total length of femur from its proximal end.

**Vastus medialis and vastus intermedius.**—As in *Mephitis* except that the area of origin of latter muscle extends over only distal 55 per cent of anterior face of femur.

**Gastrocnemius and plantaris.**—As in *Mephitis* except that gastrocnemius has a fabellum in each head, that the heads are united throughout their distal halves, and that the proximal part of the lateral head is fused with the plantaris.



**Soleus.**—ORIGIN: By muscle fibers from posterolateral face of head of fibula, and by tendon-fibers from entire length of posterior (ventral) border of fibula. INSERTION: By short (less than 2 mm. long) tendon on proximal part of calcaneus. REMARKS: The muscle is not fused with any other although it inserts almost in common with the gastrocnemius.

**Popliteus.**—ORIGIN: By strong tendon, containing a sesamoid, from lateral epicondyle of femur. INSERTION: Proximal, posteromedial 62 per cent of tibia.

**Flexor digitorum longus.**—ORIGIN: Head of fibula and by thin tendon from proximal third of posterior face of tibia. INSERTION: After union with tendon of flexor hallucis longus, by five strong tendons which insert in same manner as those of flexor digitorum profundus of hand.

**Flexor hallucis longus.**—ORIGIN: Head of fibula and all but distal 14 per cent of posteromedial face of shaft of fibula and all but distal 14 per cent of posterolateral face of tibia. INSERTION: Joins tendon of flexor digitorum longus. In my paper (*op. cit.*) dealing with the musculature of *Mephitis*, *Spilogale*, and *Martes*, an unfortunate transposition occurred. The description given for the tibialis posterior applies to the flexor hallucis longus and the description given for the flexor hallucis longus applies to the tibialis posterior. Therefore, in the third line under flexor digitorum longus, "of tibialis posterior" should read, *of flexor hallucis longus*.

**Tibialis posterior.**—ORIGIN: Narrow, triangular area, with apex at head of tibia, extending entire length of posterior face of shaft of tibia. INSERTION: Outer (toward median line of body) tuberosity of scaphoid bone.

**Peroneus longus, peroneus quinti brevis, and peroneus brevis.**—As in *Mephitis* except that origin of peroneus brevis is between proximal 33 per cent and distal 17 per cent of lateral face of shaft of fibula.

**Extensor digitorum longus.**—ORIGIN: As in *Mephitis*. INSERTION: By three tendons on bases of proximal phalanges of digits 3-5. REMARKS: The muscle is fleshy from the head of the tibia to the wrist.

**Tibialis anterior.**—As in *Mephitis* except that proximal 20 mm. (instead of 12 mm.) of medial face of fibula is included in area of origin.

**Extensor hallucis proprius.**—ORIGIN: Medial face of fibula between proximal 25 per cent and distal 33 per cent of shaft. INSERTION: By tendon on base of second phalanx (proximal phalangeal bone) of first digit. Reexamination of *Mephitis* and *Martes* shows a distinct extensor hallucis proprius to be present in each and inserting as in *Taxidea*. In both, the origin is from the medial face of the tibia; in *Mephitis* between the proximal 21 per cent and the distal 64 per cent, and in *Martes* between the proximal 40 per cent and the distal 53 per cent.

**Extensor digitorum brevis.**—ORIGIN: Lateral and dorsal faces of calcaneus and annular ligament of wrist. INSERTION: By four tendons which extend to lateral sides of digits 1–4 and join the lateral margins of the tendons of the extensor digitorum longus at the bases of the proximal phalanges.

**Flexor digitorum brevis.**—As in *Mephitis* except that there are five tendons, all of which are fleshy. The tendon to the first digit is the largest.

**Accessorius.**—ORIGIN: Distal (toward toes) 11 mm. of lateral face of calcaneus. INSERTION: As in *Mephitis*. REMARKS: The muscle is of uniform width, 10 mm., and fleshy throughout.

**Adductor ossis metatarsi quinti.**—ORIGIN and INSERTION: As in *Mephitis*.

**Adductor muscles of foot, first deep layer.**—As in *Mephitis*.

**Adductor muscles of foot, second deep layer.**—Double-headed as usual and present on each of the five digits except the first which has but one head inserting on it. What normally would be the second head, inserts on the medial side of the second digit making three heads, in all, on that digit.

The following muscles, known to occur in *Mephitis*, or *Martes*, or in both, were especially looked for in *Taxidea* but were not found. Omohyoideus, stylohyoideus, coracobrachialis, director ani superior, director ani inferior, caudofemoralis, presemimembranosus, lumbricales of hind foot, abductor and adductor medius digiti quinti, and adductor medius digiti pollicis.



VARIATION WITHIN A BROOD OF  
PACIFIC GARTER SNAKES

BY

EDNA M. FISHER

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 9, pp. 221-229, 1 figure in text

Issued February 17, 1928

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA



CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# VARIATION WITHIN A BROOD OF PACIFIC GARTER SNAKES

BY

EDNA M. FISHER

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

So far as can be ascertained from the literature at hand, nothing is known of the young of any of the garter snakes of the southern Pacific Coast district. Concerning the subspecies *Thamnophis sirtalis concinnus* and *T. s. parietalis* the reports of young so far discovered are from Iowa, Washington, and British Columbia. Ruthven (1908) gives the following data for two broods of *Thamnophis s. parietalis*. First, on September 30, a large female from Iowa gave birth to seventy-three young (*op. cit.*, p. 166); second, a female from Pullman, Washington, gave birth to eleven young (*op. cit.*, p. 169). Patch (1922, p. 78) states that a female of the subspecies *T. s. concinnus* from British Columbia gave birth to a brood of eighteen young.

## OBSERVATIONS

A Pacific garter snake, *Thamnophis sirtalis infernalis* (Blainville), was brought to the Museum laboratory on June 19, 1926, with a number of gopher snakes, all of which were captured the latter part of April or the first part of May, 1926, in the vicinity of Modesto, Stanislaus County, California. The garter snake and one gopher snake of considerable size were put in a cage used only for snakes. They lived peacefully together, were fed occasionally during the summer, and were allowed plenty of water and fresh air.

About nine o'clock on the morning of August 5, 1926, a young garter snake was discovered in the cage, and others appeared in rapid succession to the number of fifty-two, the last being born a little before noon. The young snakes were so active and numerous that despite the writer's efforts there was danger of their escaping. The mother garter snake crawled slowly about the cage and at irregular intervals, with slightly raised tail, left behind her a young snake. The young

snakes were thus "dropped" indiscriminately around the cage and they were caught and preserved as museum specimens with the exception of two. They represent various stages, from those tightly coiled on the yolk mass within the egg membranes to those with partly shed skins.

The period of gestation can be estimated as covering approximately three months, namely May, June, and July. Even a longer period than this was possible, since fertilization would have had to occur before the capture in April or the first of May.

When born the young snakes were coiled within the embryonic membranes. Some of them were attached to a heavy yolk mass by a relatively long, slender, transparent yolk stalk, while others had the yolk mass broken and only the membranes were left. Most of the young snakes were not long in escaping from the egg membranes. With rapid jerks and darts about the cage they soon freed themselves of all the various attachments of yolk and egg. When free the next thing was the shedding of the skin which was done in the usual way, peeling from the head backwards and leaving the old skin wrong side out. The tendency of the young was to seek the darker corners of the cage, some even finding seclusion under the gopher snake. The mother garter snake did not seem to be in the least interested in her numerous young ones and the gopher snake paid not the slightest attention to them.

## DESCRIPTION

Of the fifty preserved specimens, six were left in the coiled condition, while forty-four are available for measurement. The various data taken are as follows: (1) total length in centimeters, (2) the number of dorsal scale rows in the anterior region, (3) the number of supralabials, (4) the number of infralabials, (5) the number of ventral scutes intervening between the anus and the umbilicus, (6) the number of scutes involved in the umbilicus. Although it is customary to record the number of ventral and subcaudal scutes, this was found to be impossible in the present instance without removing the partly shed skin.

### SCALE ROWS

The number of dorsal scale rows is relatively constant: forty-two of the forty-four snakes have nineteen rows, while the other two have eighteen each. The first three lateral scale rows on each side are of a plain light color. In the fourth row the scales alternate dark and light. There may be slight variations in color in the fourth scale row.

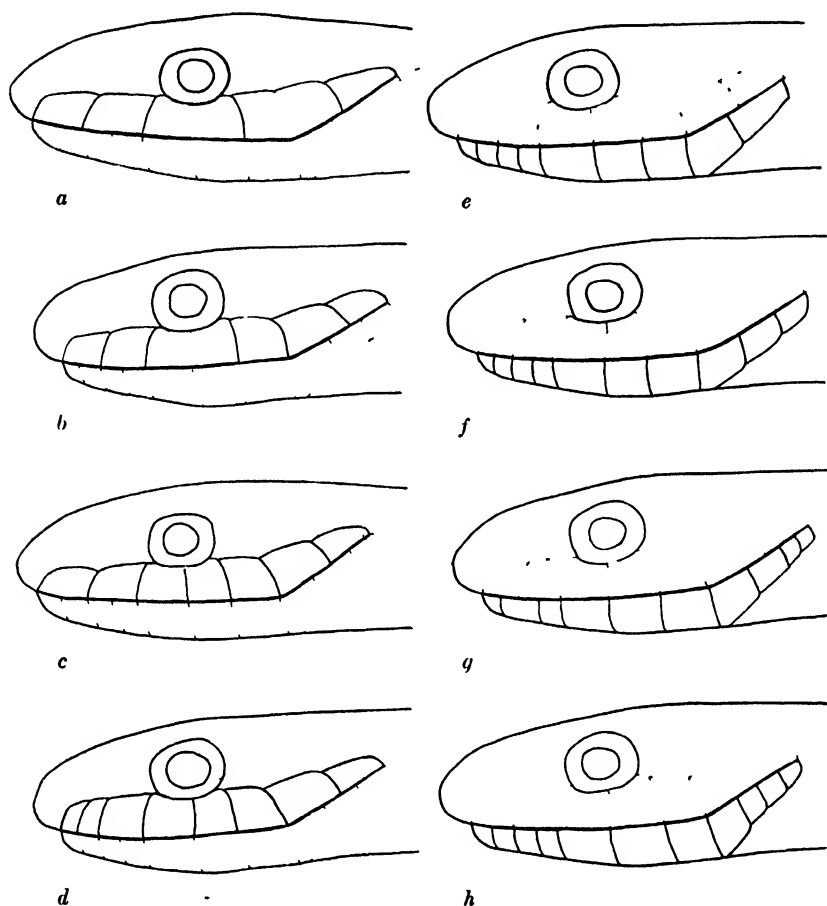


Fig. 1. Supralabial and infralabial formulae of young garter snakes. *a*, supralabial formula of five; *b*, supralabial formula of six; *c*, supralabial formula of seven, "normal"; *d*, supralabial formula of eight; *e*, infralabial formula of ten; *f*, infralabial formula of ten, "normal"; *g*, infralabial formula of ten; *h*, infralabial formula of eleven.

The fifth, sixth, seventh, and eighth scale rows are a solid dark color, and in this series is usually found the variation, if any, in the number of scale rows. In the ninth row the lateral half of each scale is dark and the dorsal half is light. The tenth scale row is all light and forms the dorsal line.

#### LABIALS

Van Denburgh (1922) in his study of one hundred and thirty-five specimens of the subspecies *Thamnophis sirtalis infernalis* found great variation in the labial formulae: for the supralabials, one hundred and four specimens with seven-seven, seventeen with seven-eight, eight



with eight-eight, and one with nine-nine. Thus eighty per cent have the "normal" supralabial formula. For the infralabials: one hundred and ten of the one hundred and thirty-five have the formula ten-ten, thirteen have nine-nine, two have ten-eleven, and two have nine-eight. It is also of interest to note the amount of variation within the brood of eleven belonging to the female *T. s. parietalis* from Pullman, Washington. The mother had seven supralabials and ten infralabials, while eight of the young had a nine-nine and three had a nine-eight infralabial formula. Ten young had seven-seven supralabials and one had a six-seven formula. It would seem that there is marked variation within a subspecies and an equally great variation within individual broods of garter snakes.

Within the brood observed there is frequent variation in the number of supralabials, and also in the position where this variation occurs. The formula most frequently found is seven: scales one and two anterior to the eye, three and four below the eye, and five, six, and seven posterior to these (fig. 1c). Some of the variations found are: (1) the fusion of scales three and four (those just below the eye) forming one large scale, the fusion of five and six (those just posterior to the eye) forming a large scale and giving the formula of five (fig. 1a); (2) the fusion of three and four, the rest remaining "normal," thus reducing the formula to six (fig. 1b); (3) the division of the first supralabial into two scales and the rest "normal," resulting in eight supralabials (fig. 1d). Not only is there this marked variation in the supralabial formula but the right and left sides vary independently. One individual has six supralabials on the left side and only five on the right. There are two with a six-six formula, one with six on the left and seven on the right, three with six on the left and eight on the right, again only one with seven on the left and six on the right, while there are twenty individuals with a seven-seven formula. There are six with seven on the left and eight on the right, one with eight on the left and six on the right, five with eight on the left and seven on the right, and five with eight on each side. From the above data it would seem that the seven-seven formula is the "normal" supralabial formula, though the study of a greater number of individuals of the same subspecies might prove it otherwise.

The conditions found in the infralabials are similar to those mentioned above for the supralabials except that the infralabials do not seem to vary so much or so often. The "normal" formula of the

infralabials is ten-ten, with scales one, two, three, and four anterior to the eye and corresponding to supralabials one and two; scales five and six below the eye, corresponding to supralabials three and four; scales seven, eight, nine, and ten posterior to the eye, corresponding to the supralabials five, six, and seven (fig. 1f).

Some of the more frequent variations found in the infralabial formulae are: (1) the fusion of nine and ten, thus reducing the formula to nine (fig. 1e); (2) the fusion of two and three, but with the division of ten into two parts, thus maintaining the "normal" of ten (fig. 1g); (3) the division of nine into two smaller scales, increasing the formula to eleven (fig. 1h). There are four young snakes with

TABLE 1  
RANGE OF LABIAL VARIATION

| Supralabials |       |                       | Infralabials |       |                       |
|--------------|-------|-----------------------|--------------|-------|-----------------------|
| Left         | Right | Number of individuals | Left         | Right | Number of individuals |
| 6            | 5     | 1                     | 9            | 9     | 4                     |
| 6            | 6     | 2                     | 9            | 10    | 10                    |
| 6            | 7     | 1                     | 10           | 9     | 8                     |
| 6            | 8     | 3                     | 10           | 10    | 21                    |
| 7            | 6     | 1                     | 11           | 9     | 1                     |
| 7            | 7     | 20                    | 11           | 10    | 1                     |
| 7            | 8     | 6                     |              |       |                       |
| 8            | 8     | 1                     |              |       |                       |
| 8            | 7     | 5                     |              |       |                       |
| 8            | 8     | 5                     |              |       |                       |

nine infralabials on the left and nine on the right, ten have the formula nine left and ten right, eight with ten left and nine right, while twenty-one individuals have the ten-ten formula. One snake has eleven on the left side and nine on the right, and another one eleven left and ten right.

When studying the individual combinations of supra- and infralabial formulae and checking the number of individuals within each combination there seem to be unlimited possibilities, with each individual snake a law unto itself. It is almost impossible to choose any particular group of formulae as "normal." Yet grouping them according to the supralabial formulae, three groups may be recognized, those with sixes, those with sevens, and those with eights. The results are shown in the following table.

This arbitrary division results in the six group with seven individuals, the seven group with twenty-seven individuals, and the eight group with eleven. From the above table it would seem that the formulae of seven and ten predominate. It is interesting to note here that the mother of this brood of young snakes has the formulae, supralabials eight-eight, infralabials ten-ten. There are only four offspring that are like the mother in this respect.

TABLE 2  
GROUPS BASED ON INDIVIDUAL LABIAL FORMULAE

| Supralabials<br>left right |   | Infralabials<br>left right |    | Number of individuals<br>in each group |                |
|----------------------------|---|----------------------------|----|--|----------------|
| 6                          | 6 | 9                          | 10 | 1                                      |                |
| 6                          | 6 | 9                          | 9  | 1                                      |                |
| 6                          | 8 | 9                          | 9  | 1                                      |                |
| 6                          | 5 | 9                          | 10 | 1                                      |                |
| 6                          | 7 | 10                         | 9  | 1                                      |                |
| 6                          | 8 | 10                         | 10 | 2                                      |                |
|                            |   |                            |    | Total                                  | 7 individuals  |
| 7                          | 7 | 10                         | 10 | 8                                      |                |
| 7                          | 7 | 9                          | 9  | 1                                      |                |
| 7                          | 6 | 9                          | 10 | 1                                      |                |
| 7                          | 8 | 10                         | 9  | 1                                      |                |
| 7                          | 8 | 10                         | 10 | 4                                      |                |
| 7                          | 8 | 9                          | 10 | 1                                      |                |
| 7                          | 7 | 10                         | 9  | 4                                      |                |
| 7                          | 7 | 9                          | 10 | 6                                      |                |
| 7                          | 7 | 11                         | 10 | 1                                      |                |
|                            |   |                            |    | Total                                  | 27 individuals |
| 8                          | 7 | 10                         | 10 | 3                                      |                |
| 8                          | 7 | 11                         | 9  | 1                                      |                |
| 8                          | 7 | 10                         | 9  | 1                                      |                |
| 8                          | 6 | 9                          | 9  | 1                                      |                |
| 8                          | 8 | 10                         | 9  | 1                                      |                |
| 8                          | 8 | 10                         | 10 | 4                                      |                |
|                            |   |                            |    | Total                                  | 11 individuals |

In comparison, the data furnished by Patch (1922) for *Thamnophis sirtalis concinnus* are as follows: thirteen individuals with the formulae, supralabials seven-seven, infralabials ten-ten; one had supralabials six left and seven right, infralabials ten on the left and nine on the right; two of the young and the parent had supralabials eight on the left and seven on the right, infralabials ten-ten. The number of young is smaller but the amount of variation is very much less in *T. s. concinnus* than in *T. s. infernalis* observed.

## GASTROSTEGES

The number of gastrosteges occurring between the anus and the umbilicus varies almost as much as the number of labials. Also, the number of gastrosteges involved in the umbilicus varies. There is one snake with fifteen gastrosteges between umbilicus and anus, ten snakes have seventeen gastrosteges, twenty have eighteen, five have nineteen, four have twenty, two have twenty-one, and only one has twenty-two. Eighteen is the most frequent number, occurring in twenty individuals. In general the umbilicus occupies two gastrosteges, though there is one specimen where only one gastrosteg is involved and several where three and sometimes four scutes are concerned. As before stated, it was impossible to count the number of ventral and subcaudal scutes and in a few instances also those between the anus and umbilicus.

## LENGTH

The average length of all the snakes measured is 19.77 cm., but they range in length from 15.45 to 21.6. Ignoring decimals we have one 15 cm. long, one 16, three 17, four 18, twelve 19, fifteen 20, and eight 21 cm. Of this particular brood more individuals fall into the length groups 19 and 20 than any other, and there are six snakes that measure 20.5 cm. The following table shows the distribution of individuals according to length.

TABLE 3  
VARIATION IN LENGTH

| 15 cm | 16 cm | 17 cm    | 18 cm               | 19 cm       | 20 cm | 21 cm |
|-------|-------|----------|---------------------|-------------|-------|-------|
|       |       |          |                     |             | 20 75 |       |
|       |       |          |                     |             | 20 7  |       |
|       |       |          |                     |             | 20 65 |       |
|       |       |          |                     | 19 85       | 20 6  |       |
|       |       |          |                     | 19 75       | 20 6  |       |
|       |       |          |                     | 19 7        | 20 5  |       |
|       |       |          |                     | 19 7        | 20 5  |       |
|       |       |          |                     | 19 6        | 20 5  | 21 6  |
|       |       |          |                     | 19 6        | 20 5  | 21 5  |
|       |       |          |                     | 19 6        | 20 5  | 21 5  |
|       |       |          |                     | 19 55       | 20 5  | 21 4  |
|       |       |          | 18 95               | 19 5        | 20 3  | 21 4  |
|       |       | 17 7     | 18 7                | 19 5        | 20 05 | 21 3  |
|       |       | 17 6     | 18 35               | 19 15       | 20 0  | 21 0  |
| 15 45 | 16 15 | 17 4     | 18 1                | 19 0        | 20 0  | 21 0  |
| 1     | 1     | Num<br>3 | ber of individ<br>4 | uals:<br>12 | 15    | 8     |

TABLE 4

DATA AVAILABLE FOR EACH INDIVIDUAL SNAKE

| Museum number | Dorsal scale rows | Supralabials |       | Infralabials |       | Number of scutes between umbilicus and anus | Scutes involved in the umbilicus | Total length in cm. |
|---------------|-------------------|--------------|-------|--------------|-------|---|----------------------------------|---------------------|
|               |                   | Left         | Right | Left         | Right |   |                                  |                     |
| 10419         | 19                | 8            | 6     | 9            | 9     | 22  | 3                                | 17.4                |
| 10420         | 19                | 8            | 8     | 10           | 10    | 20  | 2                                | 17.7                |
| 10421         | 19                | 7            | 7     | 10           | 10    | 18  | 2                                | 21.0                |
| 10422         | 19                | 7            | 7     | 10           | 10    | 18  | 2                                | 20.5                |
| 10423         | 19                | 7            | 8     | 10           | 9     | 21  | 1                                | 21.4                |
| 10424         | 19                | 6            | 7     | 10           | 9     | 18  | 2                                | 20.0                |
| 10425         | 19                | 8            | 7     | 10           | 10    | 18  | 2                                | 19.85               |
| 10426         | 19                | 7            | 8     | 9            | 10    | 17  | 2                                | 18.7                |
| 10427         | 19                | 7            | 7     | 9            | 10    | 17  | 2                                | 21.3                |
| 10428         | 18                | 7            | 7     | 10           | 10    | 18  | 2                                | 18.1                |
| 10429         | 19                | 7            | 7     | 9            | 10    | 18  | 2                                | 20.6                |
| 10430         | 18                | 8            | 7     | 10           | 9     | 17  | 2                                | 19.6                |
| 10431         | 19                | 7            | 7     | 9            | 10    | 17  | 2                                | 21.6                |
| 10432         | 19                | 6            | 8     | 10           | 10    | 21  | 2                                | 19.75               |
| 10433         | 19                | 6            | 6     | 9            | 10    | 18  | 2                                | 21.4                |
| 10434         | 19                | 7            | 7     | 9            | 10    | 15  | 2                                | 20.05               |
| 10435         | 19                | 7            | 7     | 10           | 10    | 17  | 2                                | 20.5                |
| 10436         | 19                | 7            | 7     | 9            | 10    | 19  | 3                                | 19.6                |
| 10437         | 19                | 7            | 7     | 10           | 10    | 20  | 2                                | 20.5                |
| 10438         | 19                | 8            | 8     | 10           | 9     | 18  | 2                                | 19.0                |
| 10439         | 19                | 6            | 8     | 9            | 9     | 18  | 2                                | 18.95               |
| 10440         | 19                | 7            | 7     | 10           | 10    | 17  | 2                                | 21.5                |
| 10441         | 19                | 7            | 7     | 10           | 9     | 19  | 2                                | 20.5                |
| 10442         | 19                | 8            | 7     | 10           | 10    | 17  | 3                                | 19.7                |
| 10443         | 19                | 7            | 7     | 9            | 10    | 20  | 2                                | 20.0                |
| 10444         | 19                | 7            | 7     | 11           | 10    | 18  | 3                                | 20.5                |
| 10445         | 19                | 7            | 7     | 10           | 9     | 17  | 2                                | 19.55               |
| 10446         | 19                | 8            | 7     | 10           | 10    | 18  | 2                                | 20.7                |
| 10447         | 19                | 7            | 8     | 10           | 10    | 18  | 2                                | 18.35               |
| 10448         | 19                | 7            | 7     | 10           | 9     | 19  | 3                                | 16.15               |
| 10449         | 19                | 7            | 8     | 10           | 10    | 20  | 2                                | 20.75               |
| 10450         | 19                | 8            | 8     | 10           | 10    | 18  | 2                                | 20.5                |
| 10451         | 19                | 7            | 7     | 10           | 10    | 19  | 2                                | 19.7                |
| 10452         | 19                | 8            | 8     | 10           | 10    | 18  | 2                                | 19.6                |
| 10453         | 19                | 7            | 7     | 10           | 9     | 18  | 2                                | 20.3                |
| 10454         | 19                | 8            | 8     | 10           | 10    | 18  | 5                                | 15.45               |
| 10455         | 19                | 6            | 5     | 9            | 10    | 17  | 2                                | 21.5                |
| 10456         | 19                | 6            | 8     | 10           | 10    | 18  | 3                                | 19.15               |
| 10457         | 19                | 6            | 6     | 9            | 9     | 18  | 2                                | 21.0                |
| 10458         | 19                | 7            | 8     | 10           | 10    | 18  | 2                                | 19.5                |
| 10459         | 19                | 8            | 7     | 11           | 9     | 18  | 2                                | 19.5                |
| 10460         | 19                | 7            | 6     | 9            | 10    | 19  | 2                                | 17.6                |
| 10461         | 19                | 7            | 7     | 9            | 9     |   |                                  | 20.65               |
| 10462         | 19                | 7            | 7     | 10           | 10    | 17  | 2                                | 20.6                |
| 10463         | 19                | 7            | 8     | 10           | 10    |   |                                  |                     |

## SUMMARY

The variation within this one brood of *Thamnophis sirtalis infernalis* is very great. It might be said that, in general, a "normal" appears, about which they all vary; this normal individual has nineteen dorsal scale rows, seven left and seven right supralabials, ten left and ten right infralabials, with eighteen scutes between umbilicus and anus, and with an approximate length of 20 cm. when born.

Of all the specimens only three are normal, and five are normal in all respects except the variation in number of scales occurring between the umbilicus and the anus. The remaining snakes vary in one or more points about the assumed "normal."

## LITERATURE CITED

PATCH, C. L.

1922. Some amphibians and reptiles from British Columbia. *Copeia*, No. 111, 78.

RUTHVEN, A. G.

1908. Variations and genetic relationships of the garter-snakes. *U. S. Nat. Mus. Bull.*, 61, 1-201, v-ix, 1 pl., 82 figs. in text.

VAN DENBURGH, J.

1922. The reptiles of western North America. *Calif. Acad. Sci., Occas. Papers*, 10, vol. 2, 623-1028 128 pls.



A NEW RACE OF BLACK BEAR FROM  
VANCOUVER ISLAND, BRITISH COLUMBIA,  
WITH REMARKS ON OTHER NORTHWEST  
COAST FORMS OF EUARCTOS

BY

E. RAYMOND HALL



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 10, pp. 231-242, plates 12, 13

Issued March 2, 1928

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# A NEW RACE OF BLACK BEAR FROM VANCOUVER ISLAND, BRITISH COLUMBIA, WITH REMARKS ON OTHER NORTHWEST COAST FORMS OF EUARCTOS

BY  
E. RAYMOND HALL

(Contribution from the University of California Museum of Vertebrate Zoology)

---

In 1910, members of the expedition organized, led, and financed by Miss Annie M. Alexander, to Vancouver Island, British Columbia, obtained seven specimens of black bears. These specimens and one other subsequently procured from that island by Miss Alexander, indicate the existence there of a distinct race which may be known as

## ***Ursus americanus vancouveri*, new subspecies.**

*Type*.—Male adult, complete skeleton and skin; no. 12461, Mus. Vert Zool.; King Solomon's Basin, Vancouver Island, British Columbia; July 16, 1910; collected by E. Despard; original no. 38.

*Diagnosis* (based principally on four adult males).—A member of the *Ursus* (*Euarctos*) *americanus* group. Skull wide and moderately convex in dorsal outline, rostrum parallel sided, that is, neither attenuated nor expanded anteriorly, teeth large, color black. See measurements in table 1.

*Range*.—Vancouver Island, British Columbia.

*Specimens examined*.—Total number 8, from following localities on Vancouver Island: Errington, 1; Englishman's River, 1; King Solomon's Basin, 2; Mount Douglas, 2; Nootka Sound, 1; Sproat Lake, 1.

*Comparison with, and notes on, related forms*.—Because no specimens from the mainland adjacent to, and directly opposite, Vancouver Island have been seen, the eastern limit of the range of *Ursus americanus vancouveri* has not been determined. Possibly this race occurs on the mainland too.

Variation due to age in the skulls of *Euarctos* (relative to certain other groups of Carnivora) is great. On this account table 1 is composed of measurements of adults believed to be males, all of comparable ages excepting nos. 8332 and 12655, which are very old. Unless otherwise stated, the differential characters ascribed to the several subspecies here dealt with are drawn from adult males only and may therefore not apply, in all cases, to females and young males.

From table 1 it may be seen that the large ratio to the basilar length of the zygomatic breadth, of the mastoid breadth, and of the length of the tooth row of *Ursus americanus vancouveri* are especially distinctive. It may also be noted that the rostrum, measured across the canines, is only about one sixtieth wider than where measured just posterior to the bases of the canines. The other races of black bear in northwestern North America, excepting *U. a. perniger* from Kenai Peninsula, Alaska, in which the rostrum is much attenuated anteriorly (see measurements in table 1), have the rostrum greatly expanded above the canines. The articular condyle of the lower jaw intersects a straight line passing from the tip of the coronoid process to the tip of the angular process. In *U. a. perniger* the articular condyle lies anterior to this line; in *U. a. altifrontalis* the condyle barely touches the line and in some specimens may not touch it.

*Ursus americanus altifrontalis*, the geographically adjacent race on the south, may be distinguished from *U. a. vancouveri* by the high frontal region. In no. 4678, Mus. Vert. Zool. (labeled ♀ but probably ♂, and the only adult skull available from the range of *U. a. altifrontalis*), the extreme convexity of the dorsal outline of the skull, viewed laterally, is fully as great as in the type-specimen of this race (see Elliot, 1899, pl. 43).

*Ursus americanus cinnamomum* Audubon and Bachman, of the northern Rocky Mountain region, as represented by no. 14709, Mus. Vert. Zool., from Upper Geyser Basin, Yellowstone National Park, Wyoming, has a larger skull and smaller teeth than *U. a. vancouveri*. Also the frontal shield is sulcate, the dorsal outline of the rostrum, viewed laterally, is decidedly more convex, and the rostrum is greatly expanded anteriorly above the canines.

The race from the mainland of British Columbia, as represented by no. 31017, Mus. Vert. Zool., from the telegraph line 122 miles south of Telegraph Creek, British Columbia, has: small teeth; less widely spreading zygomatic arches than *U. a. vancouveri*; rostrum expanded anteriorly above canines. The dorsal outline of the skull is in general like that of the other northwestern coastal races of black bear, but enough differences are evident, and confirmed as of geographic significance by skulls of other ages from the same region, to mark it as a race distinct from the coastal forms. Without skulls of *U. a. americanus* from eastern United States for comparison, the assignment made of these specimens from Telegraph Creek to *U. a. americanus* must be regarded as tentative. At an rate they, together

with *U. a. cinnamomum* and *U. a. altifrontalis*, show the Vancouver Island form to be distinct from its geographic neighbors on the south, east, and northeast.

Directly north is the white bear (*Ursus kermodei* Hornaday) from Gribble Island and vicinity. Mr. Francis Kermode, Director of the Provincial Museum of Natural History, has kindly sent on loan three skulls of this form: two males from Princess Royal Island and one female from Gribble Island. Mr. F. W. Miller of the Colorado Museum of Natural History has loaned two more, a male and a female, presumably taken near Port Essington, British Columbia. As compared with *U. a. vancouveri*, the skull of *U. kermodei* is smaller and narrower, the rostrum is relatively more expanded anteriorly above the canines, the frontal region is less inflated, and the dorsal outline is longitudinally less convex. Figures, measurements, and descriptions of other skulls of *U. kermodei* given by Allen (1909, pp. 233-238, figs. 1-4) bear out the differences just cited.

As clearly shown by the skull and dentition, *Ursus kermodei* is a member of the *Ursus* (*Euarctos*) *americanus* group. The material seen permits the following description of the skull: smaller than in any of the adjacent races, relatively narrow, rostrum expanded anteriorly over canines, rostrum of lesser relative and actual depth (measured at anterior point of nasals) than in adjacent forms, frontal shield slightly convex transversely, frontal region low, highest point of skull located relatively far posteriorly, teeth relatively large.

Allen (*op. cit.*, p. 237) describes the skull as more convex in dorsal outline than skulls of Alaskan specimens. The material seen by the writer indicates the reverse to be true. Probably Allen's statement was made on the basis of his comparison of the figured (Allen, *op. cit.*, fig. 4) specimen said to be from Kenai Peninsula. That specimen does have the dorsal outline of the skull less convex, longitudinally, than in *U. a. kermodei*. But ten other skulls examined from Kenai Peninsula show the race there (*U. a. perniger*) to have the dorsal outline of the skull longitudinally convex to a degree far surpassing that seen in *U. a. kermodei* (see pl. 13, *a, c*) and second only to that seen in *U. a. altifrontalis*.

From *Ursus americanus emmonsii*, as defined below, which geographically adjacent race is in cranial characters most similar, *U. a. kermodei* is readily distinguished by its: relatively and actually larger teeth, especially  $Pm^4$ ; and lesser depth of rostrum, measured at the anterior end of the nasals. These two characters readily distinguish

the females and young specimens as well as the adult males. The low frontal region, small size over all, and the seemingly greater length of the nasal bones also distinguish *U. a. kermodei* from *U. a. emmonsii*.

Thus the name *Ursus kermodei* Hornaday is applicable to a geographic race of *Ursus americanus* distinguished by the cranial characters just mentioned. Several of these cranial characters (size of teeth, degree of convexity of frontal shield, and degree of expansion of the rostrum anteriorly) are as would be expected on *a priori* grounds; that is, they are as would be expected if one were to judge by the stages of development of the mentioned structures in the bears of Alaska, in those farther south in southern Washington, and in those on Vancouver Island. Therefore, although the writer has seen skulls of only white specimens from the range of *U. a. kermodei* he infers that the cranial characters of the black and cinnamon bears there are the same and that the white color is merely a color phase and in no wise a specific or subspecific character. For records of occurrence of the white phase see Allen (1909, pp. 237, 238) and Kermode (1925, pp. A12, A13).

Study of the series of blue bears in the Museum of Vertebrate Zoology leads the author to conclude, as Swarth (1911, p. 147) did after a study of the same material, that *Ursus americanus emmonsii* as originally described is only a color phase of *U. americanus*. Indeed Nelson (1918, p. 437) states that “. . . cubs representing the glacier bear and the typical-black bear have been found in the same litter . . . .” However, the skulls of most of these blue bears together with those of the black bears from the mainland of southern Alaska are subspecifically distinct. This race is most like *U. a. perniger* but in contrast to that form has the rostrum decidedly longer and inflated anteriorly over the canines. Also the upper molars are smaller and the mastoid and zygomatic breadths are greater. Some of the skulls of the blue bears from the northernmost part of the range of this color phase are strikingly like *U. a. perniger* but the others agree with specimens from Taku River and vicinity. Since the type-specimen was taken in the Saint Elias Alps, near Yakutat Bay, it almost certainly had a skull of the same type as other blue and black bears from the mainland of that region. Accordingly the name *Ursus americanus emmonsii* will apply to the race of *Euarctos* occurring on the mainland of southern Alaska.

Specimens, from Dall and adjacent islands of southeastern Alaska, referred to *Ursus americanus pugnax*, differ from *U. a. vancouveri* in

the following respects: Frontal shield decidedly more flat; skull relatively narrower; rostrum more expanded anteriorly above canines. As may be seen from table 1, specimens from the islands of southwestern Alaska show great variation in skull characters. With more material, *U. a. pugnax* possibly would lend itself to separation into several insular races.

The two other described forms of *Euarctos* from northwestern North America, *Ursus americanus perniger* Allen and *Ursus carlottae* Osgood, are represented in the collection of the Museum of Vertebrate Zoology by ten and six specimens, respectively. *U. a. perniger* is readily distinguishable from the other northwestern coastal forms by its generally narrow skull, attenuated rostrum, and highly convex dorsal outline of the skull, which feature of development reaches its maximum in the geographically remote *U. a. altifrontalis* of Washington and Oregon. *U. a. perniger* is also distinguished in that a straight line from the tip of the coronoid process to the tip of the angular process passes posteriorly to the articular condyle. This condition furnishes another analogy with *U. a. altifrontalis* in which the articular condyle is also relatively far forward.

*Ursus carlottae*, as shown by the six skulls before me, is characterized by: generally large, elongate skull with a relatively straight dorsal outline; large teeth; and long, relatively slender rostrum that is expanded anteriorly over the canines. Although the Queen Charlotte Island bear possesses well marked characters and unquestionably is geographically isolated from related forms on the mainland, its relationships seemingly are best expressed by treating it as a subspecies of *Ursus americanus*.

The northwestern coastal and insular forms of the subgenus *Euarctos*, from north to south, with their type-localities, may now stand as follows:

*Ursus americanus perniger* Allen. Homer, Kenai Peninsula, Alaska.

*Ursus americanus emmonsii* Dall. Saint Elias Alps, near Yakutat Bay, Alaska.

*Ursus americanus pugnax* Swarth. Rocky Bay, now Bobs Bay, Dall Island, Alaska.

*Ursus americanus carlottae* Osgood. Massett, Graham Island, Queen Charlotte Islands, British Columbia, Canada.

*Ursus americanus kermodei* Hornaday. Gribble Island, British Columbia, Canada.

*Ursus americanus vancouveri* Hall. King Solomon Basin, Vancouver Island, British Columbia, Canada.

*Ursus americanus altifrontalis* Elliot. Lake Crescent, Clallam County, Washington, United States.

Attention may be called to the fact that *Ursus americanus* presents one of the most striking cases of the development of different color phases known among mammals. On the mainland of the west coast of North America the cinnamon phase occurs, along with the black phase, as far north as Taku River, Alaska (see Swarth, 1911, p. 142). Thus, in the region of Gribble and Princess Royal islands, British Columbia, three color phases (see Allen, 1909, p. 238) occur together. As the specimens described by Allen (*op. cit.*, pp. 233-238) show, the light phase is not always pure white but may include yellowish rufous and bright golden rufous bands and spots. The gray or bluish phase described as *Ursus americanus emmonsii* constitutes a fourth phase. It occurs in the region between Lynn Canal and Cape Saint Elias and is known to share its range with the black phase.

According to Osgood (1909, p. 3), "It is very significant . . . that the cinnamon phase so well known in other parts of the black bear's range is unknown on the coast of Alaska. That a gray phase may represent it there [coast of Alaska between Lynn Canal and Cape Saint Elias] certainly is not impossible." Swarth (*op. cit.*, p. 147) remarks: "That as a gray phase of the bear it replaces in Alaska the cinnamon phase is not borne out by the facts, however; for as mentioned above brown colored examples of *U. americanus* are of fairly common occurrence on the southern mainland coast." In justice to the possibility mentioned by Osgood it may be pointed out that although bears of the cinnamon phase occur on the mainland of Alaska, none is known to have been taken north of Taku River which is still south of the known range of the gray or blue phase. The cinnamon phase seems not to have been found on any of the islands.

## LITERATURE CITED

ALLEN, J. A.

1909. The white bear of southwestern British Columbia. Bull. Am. Mus. Nat. Hist., **26**, 233-38, 4 figs. in text.  
1910. The black bear of Labrador. Bull. Am. Mus. Nat. Hist., **28**, 1-6.

ELLIOT, D. G.

1899. Catalogue of mammals from the Olympic Mountains, Washington, with descriptions of new species. Field Columbian Mus., Publ. 32, Zool. ser., **1**, 241-76, pls. 41-60, numerous figs. in text.

[KERMODE, F.]

1925. British Columbia white bear (*Ursus kermodei*). Report of the Provincial Museum of Natural History for the year 1924 (Victoria, British Columbia), pp. A9-A13, 1 pl.

NELSON, E. W.

1918. Wild animals of North America. Published by the Nat. Geog. Soc., Washington, D. C., pp. 385-612, illustrated.

OSGOOD, W. H.

1909. A peculiar bear from Alaska. Field Mus. Nat. Hist., Publ. 138, Zool. ser., **10**, 1-3, pl. 1.

SWARTH, H. S.

1911. Birds and mammals of the 1909 Alexander Alaska Expedition. Univ. Calif. Publ. Zool., **7**, 9-172, pls. 1-6, 3 figs. in text.  
1912. Report on a collection of birds and mammals from Vancouver Island. Univ. Calif. Publ. Zool., **10**, 1-124, pls. 1-4.

*Transmitted December 6, 1927.*



TABLE 1

Selected cranial measurements, in millimeters, and percentages of basilar length of certain measurements, of adult male bears of the species *Ursus americanus*. The two skulls of *U. a. kermodei*, of which measurements are given, are in the collection of the Provincial Museum of Natural History (British Columbia, Canada). Although each is without a museum catalogue number, they may be distinguished, and identified by other students, by the dates of capture, written in ink on the skulls. The first one bears the date, June, 1908, and the second, which lacks most of the brain case, May 22, 1910.

| Mus Vert Zool Catalog No         | Sex | Locality  | Basilar length (of Hensel) | Breadth of rostrum at bases of canines | Breadth of rostrum just posterior to roots of canines | Percentage of basilar length of | Masloid breadth | Percentage of basilar length of | Zygomatic breadth | Percentage of basilar length of | Alveolar length of tooth-row, and border of canine to post border of M <sup>1</sup> | Percentage of basilar length of | Crown length of Pm <sup>1</sup> to and including M <sup>1</sup> | Crown length of M <sup>1</sup> and M <sup>2</sup> | Crown length of M <sup>2</sup> |
|----------------------------------|-----|---|----------------------------|--|---|---------------------------------|-----------------|---------------------------------|-------------------|---------------------------------|---|---------------------------------|---|---|--------------------------------|
| <i>Ursus americanus penniger</i> |     |   |                            |  |   |                                 |                 |                                 |                   |                                 |   |                                 |   |   |                                |
| 4383                             | ♂   | Lake Skalak, Kenai Peninsula, Alaska            | 261                        | 57                                     | 60  | 23                              | 131             | 50                              | 167               | 64                              | 99  | 38                              | 52 3  | 43 4  | 25 8                           |
| 4383                             | ♂   | Lake Skalak, Kenai Peninsula, Alaska            | 247                        | 58                                     | 63  | 26                              | 118             | 48                              | 155               | 63                              | 96  | 39                              | 53 8  | 43 9  | 26 2                           |
| 4760                             | ♂?  | Kenai, Kenai Peninsula, Alaska                  | 234                        | 56                                     | 61  | 26                              | 135             | 58                              | 166               | 71                              | 93  | 40                              | 52 8  | 42 5  | 25 4                           |
| <i>Ursus americanus emmonsii</i> |     |   |                            |  |   |                                 |                 |                                 |                   |                                 |   |                                 |   |   |                                |
| 4377                             | ♂   | Disenchantment Bay, Alaska                      | 262                        | 64                                     | 62  | 24                              | 145             | 55                              | 171               | 65                              | 98  | 37                              | 52 0  | 41 5  | 24 5                           |
| 4336                             | ♂   | Dangerous River, Yakutat Bay, Alaska            | 261                        | 64                                     | 59  | 23                              | 146             | 56                              | 177               | 68                              | 100   | 38                              | 53 4  | 42 2  | 26 0                           |
| 4329                             | ♂   | Anklin River, Yakutat region, Alaska            | 258                        | 61                                     | 58  | 22                              | 147             | 57                              | 178               | 69                              | 99  | 38                              | 53 4  | 42 9  | 25 7                           |
| 4726                             | ♂   | Disenchantment Bay, Alaska                      | 255                        | 61                                     | 57  | 22                              | 139             | 55                              | 171               | 67                              | 96  | 38                              | 50 2  | 39 7  | 22 9                           |
| <i>Ursus americanus pugnat</i>   |     |   |                            |  |   |                                 |                 |                                 |                   |                                 |   |                                 |   |   |                                |
| 8333                             | ♂   | Kupreanof Island, Alaska                        | 275                        | 67                                     | 62  | 23                              | 154             | 56                              | 189               | 69                              | 100   | 36                              | 55 0  | 43 4  | 25 9                           |
| 8326                             | ♂   | Mitkof Island, Alaska                           | 272                        | 71                                     | 63  | 23                              | 146             | 54                              | 194               | 71                              | 105   | 39                              | 56 9  | 45 9  | 27 9                           |
| 8322                             | ♂   | Fool's Inlet, Wrangell Island, Alaska           | 258                        | 64                                     | 64  | 25                              | 130             | 50                              | 174               | 67                              | 97  | 38                              | 55 8  | 46 6  | 28 6                           |
| 8330                             | ♂   | San Alberto Bay, Prince of Wales Island, Alaska | 254                        | 64                                     | 62  | 24                              | 127             | 50                              | 167               | 66                              | 113   | 45                              | 60 5  | 47 9  | 28 5                           |
| 8332                             | ♂   | Rocky Bay, Dall Island, Alaska                  | 262                        | 72                                     | 69  | 25                              | 160             | 57                              | 205               | 73                              | 115   | 41                              | 59 4  | 47 6  | 29 7                           |

*Ursus americanus (americanus?)*

31017 ♂ 122 mi. S. of Telegraph Creek on telegraph line, British Columbia 254 62 57 22 145 57 174 69 100 39 53 3 41 9 24 8

*Ursus americanus carlottae*

12655 ♂? Queen Charlotte Islands, British Columbia 289 77 68 23 158 55 200 69 115 40 62 2 49 3 29 7  
 16354 ♂? Queen Charlotte Islands, British Columbia 281 68 60 21 150 53 189 67 110 39 59 2 47 9 29 4  
 12656 ♂? Queen Charlotte Islands, British Columbia 280 68 63 23 140 50 170 61 110 39 59 4 48 2 29 0

*Ursus americanus kerroidei*

♂? Princess Royal Island, British Columbia 251 60 56 22 128 51 158 63 105 42 58 4 46 8 28 2  
 ♂ Princess Royal Island, British Columbia 57 54 94 56 5 45 0 27 0

*Ursus americanus vancouveri*

12463 ♂ Nootka Sound, Vancouver Island, British Columbia 258 61 60 23 145 56 192 74 101 39 56 7 47 5 27 8  
 12461 ♂ King Solomon Basin, Vancouver Island, British Columbia 245 63 62 25 135 55 181 74 101 41 56 5 44 5 27 0  
 12458 ♂ Errington, Vancouver Island, British Columbia 247 62 61 25 144 58 183 74 100 41 55 1 44 7 26 6  
 12464 ♂ Englishman's River, Vancouver Island, British Columbia 246 60 61 25 98 40 56 5 46 2 27 9

*Ursus americanus altifrontalis*

4678 ♂? Eugene City, Oregon 261 66 60 23 130 50 179 69 114 44 56 3 43 5 26 7

*Ursus americanus (cinnamomum?)*

14709 ♂ Upper Geyser Basin, Yellowstone National Park, Wyoming 266 67 61 23 136 51 188 71 101 38 54 2 42 5 25 5

## EXPLANATION OF PLATES

### PLATE 12

Three views,  $\times \frac{3}{8}$ , of the skull of the type-specimen of *Ursus americanus vancouveri*; no. 12461, Mus. Vert. Zool., adult male; King Solomon Basin, Vancouver Island, British Columbia.

*a.* Lateral view.

*b.* Dorsal view.

*c.* Ventral view.

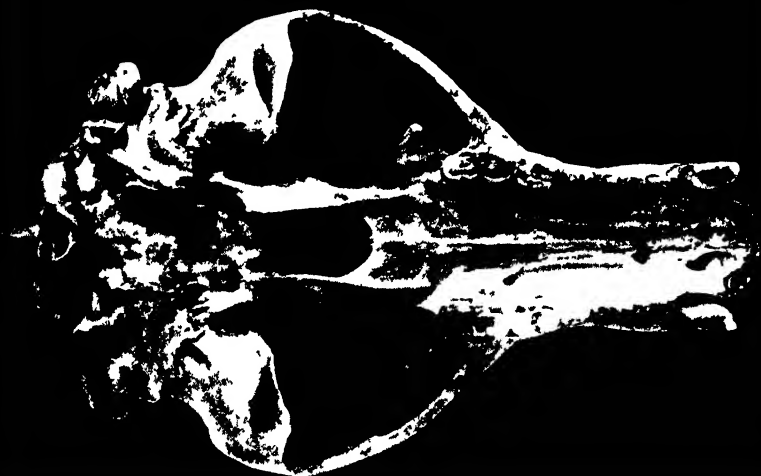
a



b



c



### PLATE 13

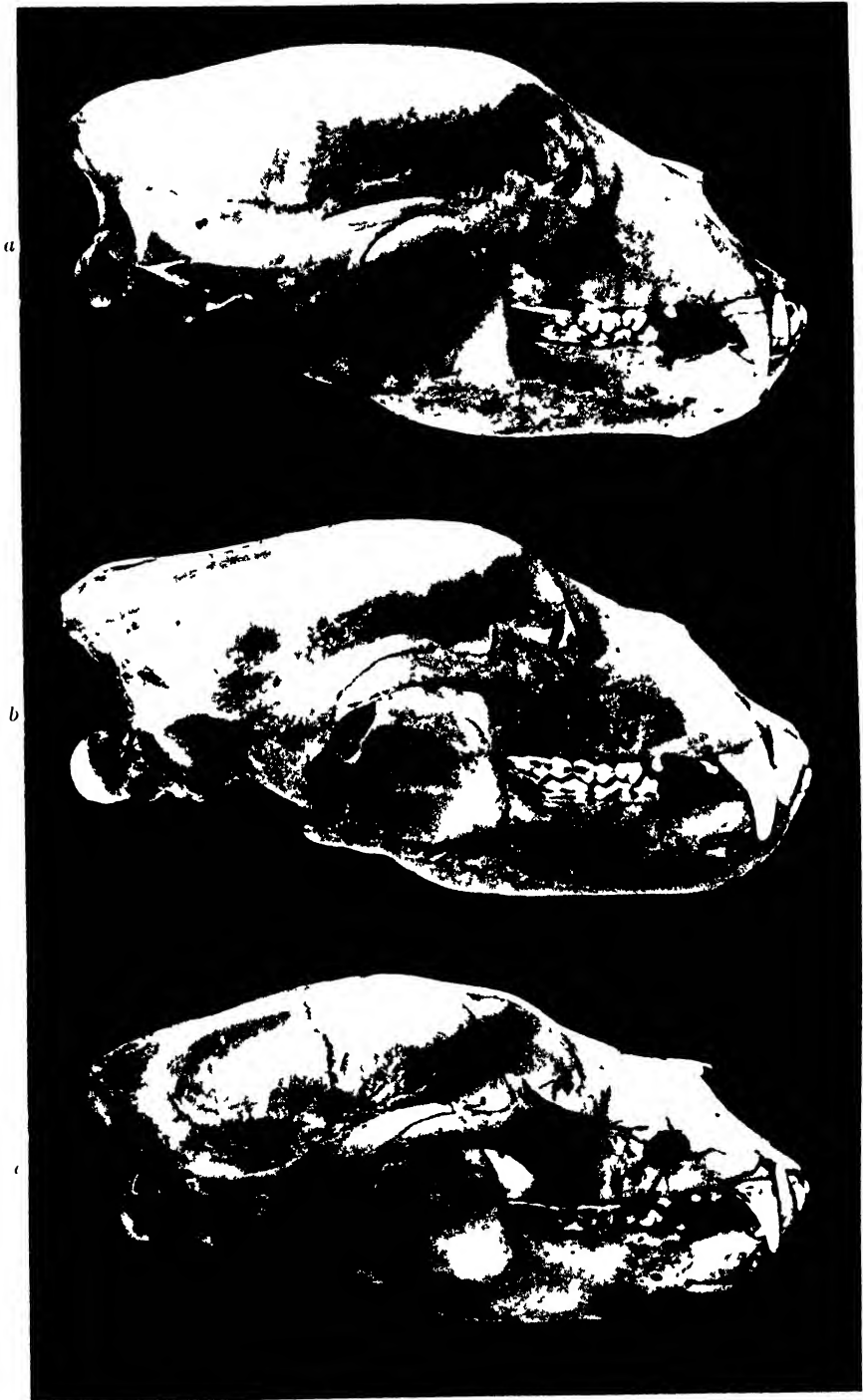
Lateral views,  $\times \frac{3}{8}$ , of skulls of *Ursus americanus*.

*a. Ursus americanus perniger*; no. 4382, Mus. Vert. Zool.; adult male; Lake Skilak, Kenai Peninsula, Alaska.

*b. Ursus americanus emmonsii*; no. 4336, Mus. Vert. Zool.; adult male; Dangerous River, Yakutat Bay, Alaska.

*c. Ursus americanus kermodei*; in collection of Provincial Mus. Nat. Hist. (Victoria, British Columbia); adult male (?); Princess Royal Island, British Columbia; June, 1908.

The figured specimens are of comparable, although not of exactly similar, ages and are regarded as typical of their respective races.





**RECORDS OF SUPERNUMERARY TEETH  
IN BEARS**

**BY  
E. RAYMOND HALL**



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 11, pp. 243-250, plates 14, 15, 1 figure in text  
Issued March 2, 1928

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# RECORDS OF SUPERNUMERARY TEETH IN BEARS

BY

E. RAYMOND HALL

(Contribution from the University of California Museum of Vertebrate Zoology)

---

Supernumerary teeth in heterodont mammals, the number of whose teeth is commonly thought of as fixed, are of infrequent occurrence and are varied as to shape, size, and place of appearance in the tooth rows. Certainly therefore such teeth are not normal structures. Neither would they seem to fall into that category of structures termed vestigial. Now if purely anatomical evidence for phylogenetic inference is properly derivable only from normal and vestigial structures, supernumerary teeth would seem to lack phylogenetic significance. On the other hand, although variable in form, such teeth are variable within prescribed limits; for instance, no accessory tooth possessing marked equine characters has been recorded in a canid. This limited variability suggests that such deviations from the normal form as are shown by accessory teeth are, in part, cases of atavism. In any event, such teeth are interesting *per se*, and from the ontogenetic point of view.

The three following described cases were the only ones found in the collection of 221 skulls of North American bears that the writer recently had occasion to rearrange in the Museum of Vertebrate Zoology. This collection consists of 100 skulls, mainly from Alaska, representing the subgenus *Ursus*, and 121 skulls, mainly from the Pacific Coast, representing the subgenus *Euarctos*.

CASE I (pl. 14).—*Ursus* (*Ursus*) *sheldoni*; male, adult; no. 970, Mus. Vert. Zool.; McLeod Harbor, Montague Island, Alaska.

Two accessory premolars, one immediately anterior to each Pm<sup>4</sup>, are present. This makes the total number of premolars above, on each side, four, a number which occurs, on both sides, in only one other of the specimens of *Ursus*, exclusive of *Euarctos*, at hand. The mentioned accessory premolars, although occurring with only three other premolars on each side, are instantly set apart as accessory teeth by their form and location. Numerous specimens with the milk dentition are available and clearly show that the teeth in question are not persistent members of that dentition.

Measured at the cingulum, the tooth of the right side is 11.5 mm. long and 6.5 mm. broad. The left tooth is 12.6 mm. long and 7.4 mm. broad and is more lateral and less anterior to  $Pm^4$  than is its opposite. Some of the bone on the lingual side of the tooth, directly above its crown, has been resorbed as a result of an abscess about the roots. This abscess involved at least the anterior root of  $Pm^4$ .

The fourth upper premolars appear to be the only teeth markedly affected by these supernumerary teeth. The form of  $Pm^4$  is normal but its position in the tooth-row is not. It has been shifted mesially. Posteriorly it has been shifted approximately one-fourth the breadth of the anterior border of  $M^1$  and anteriorly relatively more. Owing to the unequal amount of shifting, the long axis of the tooth is obliquely situated with respect to the long axis of the tooth-row. The shifting mesially, as shown in figure A, has been of sufficient amount to cause the paraconid and protoconid of  $M_7$  to occlude with the lateral, rather than as normally with the medial, face of the tritocone.



Fig. A. Lateral view of cheek-teeth of *Ursus sheldoni*, ♂, no. 970, Mus. Vert. Zool. Note the accessory premolar above and resulting non-occlusion of upper and lower teeth. The occlusion of the paraconid and protoconid of  $M_7$  with the lateral face of the tritocone of  $Pm^4$  is also shown.  $\times \%$ . Compare with figure B.

Fig. B. Lateral view of cheek-teeth of *Ursus gyas*, ♀, no. 4356, Mus. Vert. Zool. Normal occlusion where no accessory teeth are present.  $\times \%$ .

Each of the two teeth has a well developed cingulum which becomes less prominent on the anterior half of the lateral face, an incipient heel which is extended onto the posterior half of the medial face, and a single cusp with a well developed crest extending down the posterior side. Each of the two teeth presents a structural stage intermediate between  $Pm^4$  and  $Pm^3$ . For instance, the two roots are of nearly equal size, whereas in  $Pm^4$  the posterior root is the larger of the two, and in  $Pm^3$  only one root is present. The size of the accessory tooth is intermediate. Each supernumerary tooth lacks the two or more posterior, accessory cusps present in  $Pm^4$  but does have in their place a wide shelf and an incipient basin on the postero-internal face that is absent in  $Pm^3$ .

As in the two following described cases, the supernumerary teeth are regarded as having developed from anlagen distinct from those of the adjacent normal teeth.

Of the upper premolars of Carnivora known to the writer, these accessory teeth are most like the third upper premolars of *Taxidea*. This fact is perhaps of more than ordinary interest, but I should hesitate to assert that it has much atavistic import, when it is recalled that some students have claimed a near relationship between the Ursidae and Mustelidae.

CASE II (pl. 15, fig. b).—*Ursus (Euarctos) americanus* subsp. ?; adult, sex unknown; no. 4721, Mus. Vert. Zool.; probably Taku Inlet, southeastern Alaska.

What appears to be a supernumerary tooth is present immediately anterior to  $M_1$  on the right side. This tooth is situated directly opposite the normal  $Pm_4$  of the left side and would be regarded as the normal, corresponding tooth of its jaw were it not obliquely situated in the tooth-row and characterized by a different construction of the crown. The next anterior tooth seems to be the normal  $Pm_3$  although it is situated farther anteriorly than the undoubted  $Pm_4$  of the opposite jaw and measures only 10.2 mm. in length and 5.3 mm. in breadth, whereas the left  $Pm_4$  measures 11.2 mm. in length and 5.8 mm. in breadth. The supernumerary tooth is 10 mm. long and 6.5 mm. broad.  $Pm_3$  and  $Pm_1$  are present on each side. Comparison with other specimens shows that  $Pm_2$  is absent on each side.

The only visible effects that this supernumerary tooth has had on the other teeth are that  $Pm_3$ , and more particularly  $Pm_1$ , are shifted anteriorly and that  $Pm_4$  is about one-eleventh smaller than its opposite. The accessory tooth occludes with  $Pm^4$  as does  $Pm_4$  of the left side.  $Pm_4$  of the right side, by reason of its anterior position, does not occlude with any upper tooth.

The normal  $Pm_4$  has a well developed cingulum, a single median cusp with a well developed crest extending down the anterior and posterior sides, a well defined shelf-like heel posteriorly, and a smaller shelf anteriorly. The accessory tooth differs in having a lower and broader central cusp, a stronger ridge on the anterior face of the central cusp, a minute accessory cusp at the anterior margin of the tooth and a small cusp corresponding in position and form to an incipient metaconid of a molar.

The tooth is as much like the normal  $Pm_4$  of *Ursus americanus* as it is like any of the lower premolars of other Carnivora.

Because the two teeth adjacent to this accessory tooth are of normal shape (the size of  $Pm_4$  is reduced) it is regarded as having developed from a separate and distinct anlage. If the tooth here designated

as the supernumerary one be regarded as the normal tooth and the next anterior tooth as the supernumerary one, the same assumption might not be so easily made, for in that case  $Pm_4$  would be altered in shape as well as in size from the normal tooth. However, none of its parts are missing; rather, additional ones are present. Thus if we assume that division of a tooth anlage at a late embryonic period results in only part of a normal tooth being formed from one of the anlagen, we must ascribe the present case, whichever tooth be regarded as the accessory one, to the existence of two separate and distinct anlagen. If it can be proved that the fate of a tooth-anlage depends on its position, then the above assumption would be largely irrelevant as indication that no division of a single, normal anlage at a relatively late embryonic period had occurred in the present case.

The same considerations apply to the origin of the supernumerary teeth described in cases one and three. In these two cases the teeth adjacent to the supernumerary ones are normal in form; thus the supernumerary teeth might be regarded as having developed from separate and distinct anlagen.

CASE III (pl. 15, fig. a).—*Ursus* (*Ursus*) *gyas*; male, adult; no. 4386, Mus. Vert. Zool.; Snug Harbor, Alaska Peninsula, Alaska.

An  $M^3$  is present on each side. The crown surface of each is 14.5 mm. long and 13.2 mm. wide. The crown is complex. Although the cones are reduced in size the number is as great as that of the principal cusps on  $M^2$ . The anterior half of each tooth would have occluded with  $M_3$  when  $M_3$  and  $M^2$  were worn. Ordinarily, in *Ursus gyas*, the posterior border of  $M_3$  lies directly below the posterior border of  $M^2$ . The more posterior position of the posterior border of  $M_3$  in no. 4386 is due to the more than ordinary length of  $M_3$  and  $M_2$ .  $M^2$  is not shorter than usual although the posterior margin of the heel is lower than in the other specimens.

The accessory molars are single rooted. The root, as well as the crown, is triangular in cross-section. The distance between the tip of the root and the crown surface of the best developed cone is 22.5 mm. No cingulum is present. Since  $M^2$  is of normal form, except that the posterior border of the talon is slightly lower than normal, each  $M^3$  is regarded as having developed from an anlage separate from that of  $M^2$ .

The form of the accessory teeth is more suggestive of the upper molars of the Ursidae than it is of the upper molars of any other Carnivora.

In comparing the above described accessory teeth with the normal ones, occasion was taken to count the premolars above and below in 81 specimens of *Ursus* and in 100 specimens of *Euarctos*. Young specimens and those with supernumerary teeth were not included.

TABLE 1

SHOWING THE NUMBER OF PREMOLARS PRESENT IN 81 SKULLS OF *URSUS* AND  
100 SKULLS OF *EUARCTOS*

|                                 | Subgenus <i>Ursus</i> |    |    |   | Subgenus <i>Euarctos</i> |    |    |    |
|---------------------------------|-----------------------|----|----|---|--------------------------|----|----|----|
|                                 | 1                     | 2  | 3  | 4 | 1                        | 2  | 3  | 4  |
| Number of premolars above ..... | 1                     | 2  | 3  | 4 | 1                        | 2  | 3  | 4  |
| Number of specimens .....       | 1                     | 15 | 61 | 4 | 0                        | 5  | 36 | 59 |
| Number of premolars below ..... | 1                     | 2  | 3  | 4 | 1                        | 2  | 3  | 4  |
| Number of specimens .....       | 1                     | 58 | 21 | 1 | 0                        | 26 | 63 | 11 |

As may be seen from table 1, *Euarctos* averages one more premolar above and below than *Ursus*. In cases where the number of premolars of the two sides above or below were of unequal number, the specimen was entered as having the larger number. Above, 1 premolar on one side and 2 on the opposite side was found once in *Ursus* but not in *Euarctos*; 2 and 3, 13 times in *Ursus* and 5 times in *Euarctos*; 3 and 4 once in *Ursus* and 16 times in *Euarctos*. Below, 1 and 2 occurred 3 times in *Ursus* and 2 times in *Euarctos*; 2 and 3, 9 times in *Ursus* and 15 times in *Euarctos*; 2 and 4, once in *Ursus* and once in *Euarctos*.

Only once in *Ursus* and once in *Euarctos* did an unequal number of teeth occur on the two sides both above and below. Only 4 specimens of *Ursus* had 4 premolars above and only one had 4 on both sides. In *Euarctos* 4 is the usual number above and 43 specimens had 4 on each side. Below, 4 premolars occur but twice in *Ursus* and then on only one side. In *Euarctos* 4 occur in 11 specimens, 8 of which have 4 on both sides. In *Ursus*,  $Pm^4$  is absent but once and then on one side only. The same is true of  $Pm_4$ , once in *Ursus* and once in *Euarctos*.

When the number of premolars is less than four the second is generally absent. The first premolar is sometimes absent, and occasionally both the second and third are absent when both the first and fourth are present.

The number of premolars in each subgenus is correlated with age and with locality. The number in old individuals is, on the average, less than in young ones. Two series of specimens of comparable age from two localities frequently show a marked difference in the number of premolars.

Transmitted December 6, 1927.

## EXPLANATION OF PLATES

### PLATE 14

Natural size.

Occlusal view of upper molar and premolar teeth of *Ursus sheldoni*; male, adult, no. 970, Mus. Vert. Zool.; McLeod Harbor, Montague Island, Alaska. Note the accessory premolars, one lateral, one anterior to each Pm<sup>4</sup>. The resultant crowding mesially of each Pm<sup>4</sup> may also be seen.



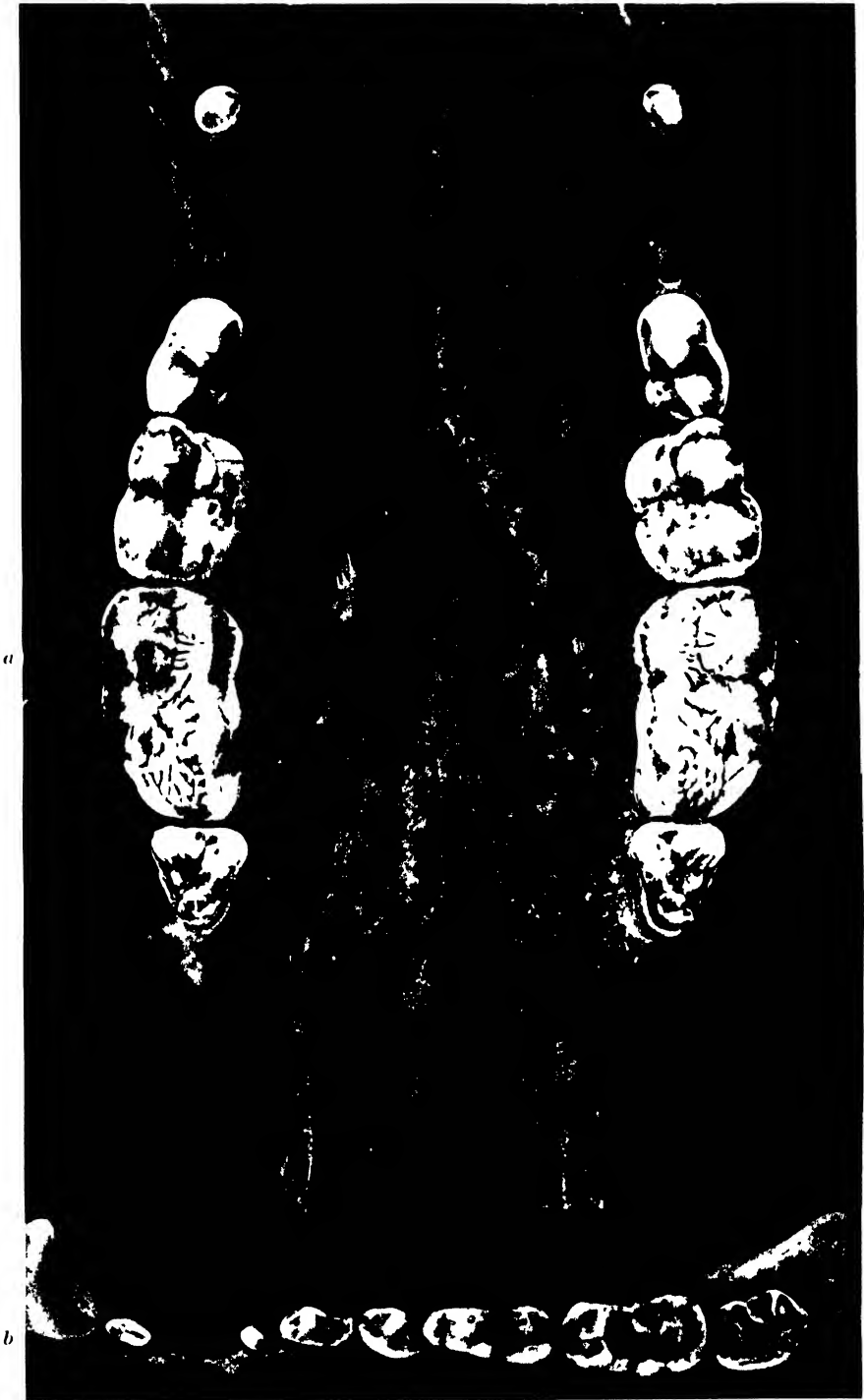


## PLATE 15

Natural size.

*a.* Occlusal view of upper molar and premolar teeth of *Ursus gyas*; male, adult; no. 4386, Mus. Vert. Zool.; Snug Harbor, Alaska Peninsula, Alaska. Note the form and position of the third (supernumerary) molars.

*b.* Occlusal view of right lower molar and premolar teeth of *Ursus (Euarctos) americanus* subsp.(?); adult, sex unknown; no. 4721, Mus. Vert. Zool.; probably Taku Inlet, southeastern Alaska. Note the accessory premolar immediately anterior to  $M_1$ . The strong ridge on the anterior face of the central cusp, the incipient metaconid-like cusp and the minute, accessory cusp at the anterior margin of the supernumerary tooth are shown.





VARIATIONS IN THE  
FOX SPARROW (*PASSERELLA ILIACA*)  
WITH REFERENCE TO NATURAL HISTORY  
AND OSTEOLOGY

BY

JEAN M. LINSDALE

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 12, pp. 251-392, plates 16-20, 38 figures in text  
Issued September 28, 1928

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# VARIATIONS IN THE FOX SPARROW (*PASSERELLA ILIACA*) WITH REFERENCE TO NATURAL HISTORY AND OSTEOLOGY

BY  
JEAN M. LINSDALE

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

## CONTENTS

|   | PAGE |
|---|------|
| Nature of the problem                                 | 251  |
| Object of studies of variation in general             | 251  |
| Need for such studies                                 | 253  |
| Previous studies of variation in birds                | 254  |
| Argument for selection of <i>Passerella iliaca</i>    | 259  |
| Objects of this particular study                      | 260  |
| Taxonomy of <i>Passerella</i>                         | 261  |
| Systematic status of the group                        | 261  |
| Subspecies of <i>Passerella iliaca</i>                | 263  |
| Natural history of <i>Passerella iliaca</i>           | 266  |
| Material and acknowledgments                          | 301  |
| Methods   | 303  |
| Preparation of specimens                              | 303  |
| Measurement   | 304  |
| Drawing   | 304  |
| Characters used                                       | 305  |
| Variations in internal structure                      | 309  |
| Weight  | 309  |
| Skeleton  | 315  |
| Correlation with variation in external characters     | 350  |
| Adaptive significance, with reference to environment  | 360  |
| Comparison of <i>Passerella</i> with <i>Melospiza</i> | 363  |
| Conclusions   | 366  |
| General summary                                       | 368  |
| Literature cited                                      | 377  |

## NATURE OF THE PROBLEM

### OBJECT OF STUDIES OF VARIATION IN GENERAL

A study of variation in any group of organisms may be carried on for its own sake, or, as is more usually the case, it may become a part of some specialized study of that group. Among the special types of ornithological study which are closely dependent upon the proper interpretation of the phenomena of variation for their soundness are systematics, evolution, and paleontology.

Every contribution to avian systematics is trustworthy to just the degree that it is based on clear, accurate, and extended examination of the facts of variation in the group with which it deals. Early systematic workers, compelled to work with few specimens, could not be expected to interpret satisfactorily the many confusing aspects of variation, which, indeed, were largely unknown to them. It is surprising, when the nature of their limitations is considered, that these early systematists made so few errors as they did. Although workers of the present in general recognize the need for basing their systematic judgments upon an adequate analysis of variation, it is too often true that their decisions are based on insufficient material or upon faulty analysis or even upon superficial examination of the material they have.

Not only is it desirable for the persons who work in systematics to understand the phases of variation of the objects with which they deal, but much confusion would be eliminated if more of the ornithologists, whose chief interest lies in other directions, could share that understanding. Possibly the many recent protests against the use of subspecific distinctions in bird studies would never have been made had their authors possessed a wider knowledge and clearer appreciation of variability in birds.

If we accept as reasonable the proposition (Jordan, 1927, p. 187) that the study of the facts of evolution is an outdoor subject, then it immediately becomes desirable to accumulate and analyze facts of variation in the kinds of organisms which are to be studied. It would seem that more significant results might be expected in studying the smallest discernible deviations within a species than in comparing larger groups which are less similar and, supposedly, less closely related if an attempt is to be made to interpret the manner or cause of the divergence of groups of organisms through space and time and to correlate this divergence with changing factors in the environment of the groups.

Of all the divisions of ornithology, paleontology, perhaps, is most dependent for good results upon a sound perspective with respect to osteological variability of every kind. Dr. Loye Miller (1912, p. 63) perceived this truth many years ago and has clearly stated the problem which confronts the avian paleontologist.

## NEED FOR SUCH STUDIES

Many writers have indicated that they recognized a need for studies such as the one here undertaken, but they have also stated that the difficulties to be encountered in such an undertaking are sufficiently great to offset its desirability. Shufeldt (1887, p. 268) with an extended experience in avian osteology pointed out the necessity for measurements and exact descriptions of bones of birds to be based on large series. The reasons given by Lucas (1893, p. 210) for the neglect of such branches of ornithology are the lack of "time, care, and patience needed for the prosecution of such work, the labor required for the accumulation of facts, and the difficulty of properly publishing results."

In the opinion of Newton (1893, p. 1003) "it behooves ornithologists . . . to learn all they can" of the facts of variation "apart from any speculation that may be raised upon them." In a criticism of Davenport's *A Precise Criterion of Species*, Allen (1898, p. 802) outlines an "ideal way" to go about making a quantitative study of variation which is almost exactly the method used in this study. He adds that "it might be well worth doing, at least in the case of a few groups, for the general bearing such results would have on the problem of evolution." He then comments that "the work and expense involved is too great" for carrying out such an undertaking. Pyecraft (1910, p. 291) has rigorously criticized those systematists who give only "average" measurements in their diagnoses of species.

The extensive investigation in problems of genetics that has occupied the attention of biologists within recent years has furnished additional incentive to investigation of variability in birds. Chapman (1923, p. 243) said that

'pedigree work,' except with domesticated species, is rarely possible with birds, and such contributions as the ornithologist can make to this subject from the study of birds in nature must be based on the examination of a sufficient number of specimens fully to illustrate the range of a species' variations with an attempt to determine their nature and their causes.

Along the same line Sumner (1923, p. 238) wrote

We are not yet prepared to frame any adequate general hypothesis as to species formation . . . let us busy ourselves with the collection of data of a sort which will be relevant to the final solution. And among these relevant data it is my belief that the facts of geographic variation will bulk as large in the end as those of Mendelian inheritance. . . . It is possible to arrive at results of genuine scientific importance, even if various issues, commonly regarded as fundamental, are for the time being left untouched.



## PREVIOUS STUDIES OF VARIATION IN BIRDS

The extensive work of Allen (1871) on the mammals and winter birds of east Florida forms not only one of the earliest but also one of the most comprehensive contributions to a knowledge of variation in mammals and birds. It is difficult to appreciate properly the results of Allen's work at present because so many of his conclusions that were innovations then have since been generally accepted and are now common knowledge. Part of that work dealt with external parts of birds which were found to vary from 15 to 20 per cent in general size and in relative size of different parts in specimens of the same species and sex taken at the same locality. According to Allen, the fact that all external parts of the body varied, implied a corresponding variation in the internal anatomy. However, no evidence was given to support this statement.

Concerning climatic variation Allen (*loc. cit.*, p. 229) wrote that it "involves as completely all parts of the animal as does individual variation. It is more marked, however, in some features than in others. The three most prominent features of climatic variation in birds are the following: variation in general size, variation in the size and form of the bill, variation in color." He also pointed out that there were "similar variations with locality occurring, to a greater or less extent, in all species having nearly the same geographical range."

Aside from the use of these data by Wallace, little was done with the great mass of facts collected by Allen and no other work of that nature was attempted, either to extend or to corroborate his results.

The work of Bumpus (1897) on the English sparrow is often cited in evolutionary books as an example of the demonstration of the relation between variation and evolution through natural selection. His work, in addition, indicated that after this bird had been introduced into America it became more variable, under the new conditions, than the original population from which it was taken in Europe. External characters were used chiefly but a few linear measurements of bones were included.

Strong (1901) attempted to apply Davenport's (1898) "precise criterion of species" in the case of a small group of variable North American birds. His data included measurements of linear dimensions, curvature of bill, and color in the smaller shrikes. The nature

of the material, small samples from widely scattered localities, prevented a thoroughly satisfactory demonstration of the method used. One of the conclusions reached in Strong's paper (p. 297), however, is pertinent here: "The contention that quantitative methods are less useful than those ordinarily employed because of the large amount of material required, is mischievous, for it argues that generalizations professing precision are possible by methods which are not precise."

The analysis of size variation in *Pyrenestes*, a genus of weaver-finches, by Chapin (1924) bears, in part, upon some of the questions considered in the present study. Chapin, after a careful study of variation in external characters, distribution and some environmental features, concludes:

1. Isolation is probably responsible for the color differences between the 3 species of *Pyrenestes*, but variation in size is dependent upon some other factor.

2. In at least 2 of the species . . . the smallest individuals inhabit those regions where there are heavy rain forests, the largest ones usually the more open savannas of the West African sub-region. They are connected by birds of intermediate size, these being found especially along the border regions of the forest country.

3. The average size of the bird's bill in any locality can be shown to give a rough index of the nature of the vegetation, or of the rainfall.

4. It seems likely that a correlation exists between the greater size of the bill and a more restricted diet of hard seeds of certain sedges.

Other writers have paid some attention to size variation in birds. Chapman (1920, p. 31) found that males of *Ostinops decumanus* are apparently more variable in size both individually and geographically than the females. Chapman and Griscom (1924, p. 282), writing of the house wrens, state that size always increases with altitude and that birds which range higher than any other forms in the same species are largest.

Dwight (1925) in his study of the gulls classed variation in size as specific, sexual, or individual. He found a constant average sexual difference in size except in two species. Within this group of birds the females show a wider range of variation in size, especially in the bill, than do the males.

Measurements of *Myiarchus cinerascens* published by Grinnell (1914, p. 148) showed a decided sexual difference in size and, in both sexes, a greater variation in size and relative narrowness of the bill than in lengths of wing and tail. He pointed out that females appeared to be subject to greater variation than males. In the same paper (p. 157) a consideration of variation in *Molothrus* resulted in

establishing these points: average is practically identical with mid-point of range in both sexes; the wing length is least variable; males are more variable than females; females are 9 per cent smaller than males in general size of body. The same author (1909, p. 278) in a consideration of the phylogenetic value of size variation in three species of *Molothrus* wrote, "A survey of the relevant cases among birds leads me to argue that as a rule mere uniform increase or decrease in size signifies less of phylogenetic separation than do changes in proportion of parts."

Variation in color tone has received attention from many writers. A fair summary of the opinions of many vertebrate zoologists may be found in these statements by Grinnell (1922, p. 14),

There is, I am sure, no question that degree of pigmentation closely parallels degree of wetness in climate. Very many distantly related groups of birds and mammals show such uniformity in this reaction that the correlation must be accepted as a fact. But "wetness" of climate is not a simple factor: it may involve humidity of the air, cloudiness, or rainfall, or any two of these, or all three.

Use of this type of variation in analysis of variation within a single species is exemplified in the following summary of the situation in *Chamaea fasciata* by Grinnell and Swarth (1926, p. 170):

Geographic variation within the species *Chamaea fasciata* consists, in so far as we can discern, entirely of modifications in tones of color. The total range of variation in this regard involves about as great differences as are to be found within any western species. But although birds from the two extremes of the wren-tit's range, as well as others from certain interlying localities, are easily distinguishable, there is difficulty in defining exact boundaries to the range of any of the described subspecies, due to the gradualness in which color changes are effected between the adjacent regions.

Comments of Dwight and Griscom (1921, p. 1) in a review of *Atlapetes gutturalis* indicate that in this species study-skins turn brown in less than thirty years and are then useless for subspecific comparison. These writers found not geographically progressive racial variation but that two closely similar races at the ends of the range were separated by an easily distinguished race. They point out that a comparable situation exists in several other Central American species.

Snodgrass (1903, p. 411) concluded from a study of *Geospiza* skulls that the species and varieties were related in a serial manner: that evolution "has not been along lines radiating from a common centre, but has consisted principally of successive modifications along one line." A study of color phases of the plumage supported this

statement. In that group it was also found (p. 414) that the sternum, shoulder girdle, and ribs showed no such modifications as the skull. It was also pointed out (p. 412) that a study of the bills of nestlings would probably be of little phylogenetic value. The same writer (1902), in a consideration of the specific and varietal characters, shape, and size of bill in thirty-four species and varieties of the Fringillid genus *Geospiza* pointed out that, since the bill is the feeding organ, the place to look for causes of its variation would be a variation in the character of the food. He preserved and examined 209 stomachs. His conclusions concerning this point were:

If it is assumed that the various sizes and shapes of bills amongst the *Geospizae* have developed as adaptations to differences in food habits, then it must be shown that the different species of the genus feed on different species of seeds. This cannot be done.

The evidence, then, seems to be in favor of the general conclusion that there is no correlation between the food and the size and shape of the bill. If this is true, then we must look elsewhere for an explanation of the variation of the *Geospiza* bill.

The several revisions of genera by Swarth have contributed importantly to a better understanding of the variation encountered in each group. Birds of the genus *Psaltiriparus* (1914, p. 502) were found to vary (1) seasonally, (2) at different ages, (3) geographically, and (4) in one species, sexually. In *Aphelocoma* (1918, p. 408) the species were found to be sharply defined and to remain uniform in appearance over a wide territory. The characters, it was stated, vary independently and not always in the same direction. In a study of some song sparrows (1923, p. 220) the point was emphasized that "all recognizable subspecies are not equidistant from one another, and they should not be treated as if they were." The work of this author on *Passerella* (1920), which served as a basis for the present study, is considered in another place. Swarth's work has dealt entirely with external characters.

The question of adaptational variation has not been emphasized, so far, in this review. It might be well to cite two recently written examples illustrating extreme points of view on this important subject. Gates (1917, p. 595) in an exposition of the mutation theory and the species concept says,

thus even in birds our second type of variation, non-adaptational and not related to local conditions, is apparently an important factor in speciation, although in *Colaptes* too geographical races occur. . . . In distribution also these species do not follow the rule for geographic subspecies, for they overlap over large areas.

Contrasted with this is the condition found by Meinertzhagen (1926) in the genus *Corvus* in which he attributes geographic differences in the genus to environmental influences. He writes (p. 59),

in all groups subspecific differences are traceable solely to environment, the more brilliant sheen of humid-tropical birds contrasting with the duller sheen of those inhabiting more temperate climates. . . . Though no Mendelian influence is traceable in the genus, some doubt must remain on two points—the colour of the iris and the shade of white or grey at the bases of the feathers.

Most of the works cited hitherto have had to do with variation in characters of external structure. The status of our knowledge of variation in muscular systems of birds has been well explained by Beddard (1898, p. 76).

Shufeldt (1888) has well summarized the difficulties to be encountered by anyone who tries to find and describe variations of a qualitative nature in the skeletons of birds. His statements probably explain why so little work of that nature has been done. At least, they form a partial explanation of why so much attention is paid, in the present study, to quantitative, rather than qualitative variation. Shufeldt's comments on this matter are here quoted rather fully because they coincide almost exactly with the present writer's experiences in similar attempts to those he described. He wrote,

. . . it is truly wonderful to note the manner in which the cranial characters, indeed the skull as a whole, in these numerous genera, morphologically shades from one series of the more intimately related forms into the group next most nearly allied, and so on along different lines, diverging as they do, from any well defined genus we may elect as our primary one for initial comparison. True as this is, however, I find it none the less true that if we critically compare the skeleton of some Finch, for instance, at one extremity of such a series, with the skeleton of another conirostral species chosen from the other, important differential characters may not infrequently be detected, which characters are constant for the species, and of great value to the taxonomist of this, in many cases, puzzling group of birds.

By the easiest sort of intergradation the skull of *Zonotrichia* shades into the skull of *Chondestes*, and an attempt to define the differences between them would simply result in an enumeration of insignificant details.

Concerning the shoulder girdles of birds Shufeldt wrote,

We have examined them in many species representing a host of different genera, and yet who has been enabled to base a single, *constant*, differential character upon the elements of this arch. . . . Differences, of course, yes, constant differences, *do* exist, but they are not of the kind which can be powerfully brought into play by the taxonomist. . . .

The statements quoted above serve to emphasize the inadequacy of qualitative descriptions in avian osteology.

ARGUMENT FOR SELECTION OF *Passerella iliaca*

In selecting a group of birds for a study such as the one here undertaken it was highly desirable to pick one that would satisfy several conditions which, it was anticipated, would give greater value to the results. There may be, and probably are, many genera of birds in which variation could be studied with more significant results than were obtained in this study, but a careful preliminary survey of the groups available indicated that a study of variation in *Passerella* might give more significant results than the others. One of the deciding factors was the existing and exceptionally complete knowledge of the variation in external characters in this group. In addition to forming a basis for a comparison of the known trends of external variation with subsequent findings as to the nature of variation in internal structure, this knowledge made it possible to select more suitable localities for collecting summer specimens than could have been done in the case of a species less well known.

In addition to the published review of this genus it was possible, throughout this study, to obtain the personal aid of Mr. H. S. Swarth, the reviewer, in identifying specimens as well as in furnishing information supplementing that in his printed work on the genus.

The study of the external characters of *Passerella iliaca* proved that there existed in external characters little variation due to age, sex, or individual. It was inferred from these facts that a lesser amount of variation of these classes might be expected in the internal structures of birds of this genus than in birds where external variations of these classes were known to be great.

Another result of the study of external characters was the demonstration of an extreme degree of geographic variation. In fact, this group is one of the most plastic in North America as shown by comparisons of populations from separated and varying environments. Here, then, is a group of birds highly variable in one respect, the one which it was desired to study especially, but with a minimal amount of variation, as shown by a thorough systematic study of the usual nature, in the other kinds of variation usually encountered. This condition favored the choice of *Passerella* for the proposed study.

One factor, the availability of material, necessarily important in this instance because of the need for saving time and expense, proved to be important in the selection of a group for study. First, the genus

is confined to North America and, in the breeding season, to mountains of western United States and northward in Canada and Alaska. All the described subspecies are found in California at some season and most of them are abundant in the proper habitats.

The associationally restricted breeding habitat of the fox sparrow made it seem possible to demonstrate correlations between variation in skeletal characters and variation in environmental factors; at least it seemed that such correlations might be looked for more profitably in a species of restricted habitat than in one with a wider range of effective environmental factors. Here, also, an opportunity was promised to study the influence of isolation upon trends of variation in internal structure.

#### OBJECTS OF THIS PARTICULAR STUDY

During the early stages of this study several questions were formulated to serve as guides in the accumulation of facts and to serve to narrow the scope of the proposed investigation: Do subspecies of *Passerella iliaca* vary in characters of internal structure? How does the amount of geographic variation in internal characters (if any) compare with age, sex, and individual variation in those characters? If present, can skeletal variations be correlated with variations that can be detected in external characters? Are the subspecific groups homogeneous or is there a gradual change in internal structure throughout their ranges? Are the subspecific groups now recognized separated by breaks in respect to characters of internal structure? Can varying skeletal structure be correlated with definite changes in behavior or changes in some environmental factors? Are quantitative skeletal characters of any use in determining the specific or generic relationships between this and related genera?

Although all these questions have not been conclusively answered, it is thought that the rather favorable material that has been available for study has made possible some definite contribution to a final answer in each case.

## TAXONOMY OF PASSERELLA

## SYSTEMATIC STATUS OF THE GROUP

Merrem in 1786 first described a member of the group herein considered and he it was who gave the name *Fringilla iliaca* to the eastern fox sparrow.

In 1837, Swainson established the genus *Passerella* as a division of *Fringilla* of Linnaeus. This he placed in the subfamily Fringillinae of the Fringillidae. In the same group and of equal rank with *Passerella* were placed *Fringilla*, *Zonotrichia*, *Ammodramus*, and *Chondestes* in the order given. *Passerella* was made to include only the form *iliaca*. Swainson's characterization (p. 288) was as follows:

*Passerella*, Sw. Bill short and perfectly conic, thick at the base, and rather abruptly pointed at the tip, which is entire. Culmen perfectly straight. Both mandibles of equal thickness. Wings moderate; the first quill shorter than the second, third, and fourth, which are the longest. Tail moderate, broad, and nearly even. Feet large, strong. Middle toe longer than the tarsus; inner toe much shorter than the outer. Claws long, slender, and but slightly curved; hinder claw as long as the toe. America.

By the time of Baird's writing in 1858 there was so much confusion in the systematic arrangement of the sparrows that he was obliged to work out the whole subject for himself. He summarized (p. 406) the situation in this way:

The systematic arrangement of the fringilline birds of the United States is more difficult than that of any other group, owing to the large number of species closely related to each other and exhibiting endless though minute variations in structure and form. Nearly all authors regularly avoid committing themselves by an attempt at the definition of their different divisions, giving only the names of types as indicative of their meaning. I have, therefore, been able to derive no aid from ornithological publications in arranging the species, and have been obliged to work out the whole subject anew from the beginning, as far as North American species are concerned.

In the system adopted I do not claim any very natural combination of species into genera, nor of genera into sub-families; all I have aimed at is to present a convenient artificial scheme by which the determination of the species may be facilitated. The means at my command are manifestly insufficient for the satisfactory solution of a problem which has puzzled the best ornithologists of the day, with all the possible resources at their command in the way of specimens and books.



Baird made use of four subfamilies:

1. Coccothraustinae
2. Spizellinae, which contained *Melospiza*
3. Passerellinae, which contained *Passerella*
4. Spizinae

His revised description of the genus *Passerella* follows:

Body stout. Bill conical, not notched, the outlines straight; the two jaws of equal depth; roof of upper mandible deeply excavated, and vaulted; not knobbed. Tarsus scarcely longer than the middle toe; outer toe little longer than the inner, its claw reaching to the middle of the central one. Hind toe about equal to the inner lateral; the claws all long, and moderately curved only; the posterior rather longer than the middle, and equal to its toe. Wings long, pointed, reaching to the middle of the tail; the tertials not longer than the secondaries; second and third quills longest; first equal to the fifth. Tail very nearly even, scarcely longer than the wing. Inner claw contained scarcely one-and-a-half times in its toe proper.

*Color*.—Rufous or slaty; obsoletely streaked or uniform above; thickly spotted with triangular blotches beneath.

Ridgway (1901)<sup>9</sup> divided the Fringillidae into eighteen groups. Zonotrichiae, the largest group in number of recognized genera, contained both *Melospiza* and *Passerella*. *Helospiza* Baird was not recognized as a genus.

A study of the palates of many fringilline genera led Sushkin (1925) to propose a rearrangement of these birds. He placed *Melospiza* and *Passerella* as adjacent genera in the family Emberizidae of the superfamily Emberizoidei. Sushkin did not have an opportunity to examine material of these particular genera.

Statements are frequently encountered in more recent bird literature which indicate that many persons have been impressed by the similarities of *Melospiza* to *Passerella*. In this connection Swarth (1920, p. 105) says:

*Passerella* is closely related to *Melospiza*. Fox sparrows are very like song sparrows, in structure, appearance, habits and actions. The respective ranges also of *Passerella iliaca* and *Melospiza melodia* are suggestive of rather close relationship between the two, for their habitats are in a measure complementary since the two species, though frequently occurring in the same general regions, occupy different life zones.

Grinnell (1908, p. 100) writes that fox sparrows "are like song sparrows in so many ways that it seems strange that they should be allotted to a separate genus." Other writers have pointed out similarities in the songs of the two species.

A complete history of the nomenclature of *Passerella iliaca* may be found in Swarth's review. Attention is therefore directed here only to the fact that for many years the genus was considered to be made up of three species.

#### SUBSPECIES OF *PASSERELLA ILIACA*

The species *Passerella iliaca* has been reviewed at greater length and with greater detail than any other of the more variable species of North American birds. Swarth with a large amount of material, 1,800 specimens, and with rich experience in dealing with the systematics of the many variable species of western American birds, was able not only to detect and define the many small differences separating the races that he recognized but he was also able, by the use of those characters, to interpret clearly a majority of the data of migration and distribution that had been assembled by the many collectors and naturalists who have been interested in fox sparrows. The review is probably more important for its elucidation of the nature of variation shown by the species and correlation of that with environment and physical barriers as pointed out by Stone (1921) than as an aid to persons of little experience who wish to identify skins. The possible dangers of such use have been explained by Taverner (1921, p. 77).

In analyzing the variation in this species Swarth found it desirable to recognize these three main groups of subspecies:

1. *iliaca*; bright reddish and clear gray; tail shorter than wing; bill of medium size.

*iliaca*  
*altivagans*

2. *unalaschensis*; reds predominating, becoming darker from north to south; grays at a minimum; tail shorter than wing; bill of medium size, diminishing from north to south. Greatest variation in color; proportions relatively uniform.

|                      |                   |
|----------------------|-------------------|
| <i>unalaschensis</i> | <i>annectens</i>  |
| <i>insularis</i>     | <i>townsendi</i>  |
| <i>sinuosa</i>       | <i>fuliginosa</i> |

3. *schistacea*; grays predominating, increasingly toward the south; reds at a minimum; tail rarely equal to, usually longer than, wing; bill extremely variable, increasing in size westward and southward. Greatest variation in proportions; color relatively uniform.

|                     |                  |
|---------------------|------------------|
| <i>schistacea</i>   | <i>canescens</i> |
| <i>fulva</i>        | <i>monoensis</i> |
| <i>megarhynchus</i> | <i>mariposae</i> |
| <i>brevicauda</i>   | <i>stephensi</i> |

The iliaca group covers more territory than either of the other two. The fact that only two races are recognized in this group may have a slight correlation with the small amount of summer-collected material available, but it is possible that, even if more thoroughly known, the races would have more extensive ranges than those of more mountainous sections of the continent.

In the unalaschcensis group Swarth found a definite line of variation accompanying continuous distribution of the species. He recognized dividing lines between the subspecies but in only one race, *insularis*, did the dividing line correspond to observed physical barriers to distribution.

In the schistacea group there is continuous variation, but Swarth's study indicated the presence of discontinuous distribution in every case. Every subspecies is separated from others by unsuitable life zones. However, his material did not show a break in variation with every gap in distribution. Later work indicates that possibly the ranges of some subspecies touch the ranges of certain adjacent ones at some localities so that there would be continuous distribution in some instances.

The following list of the commonly recognized races of *Passerella iliaca* with the type locality and summer range of each is taken from Swarth (1920) unless otherwise stated.

*iliaca* (Merrem).

Type locality.—Exact locality not known.

Range.—Breeds in Boreal zones from tree limit in northeastern Alaska, northern Mackenzie, central Keewatin, northern Ontario (Moose Factory), and northern Ungava south to central Alberta, northern Manitoba, southern Keewatin, Magdalen Islands, and Newfoundland. (A. O. U. Checklist, 1910, p. 277.)

*altivagans* Riley.

Type locality.—Moose Branch of Smoky River (about 7,000 feet altitude, Alberta.

Range.—Known only from a few points in the interior of British Columbia and the adjacent part of Alberta. Moose Pass, Jasper Park, Alberta; Thudale Lake, McGillvary Creek, and Mt. McLean, Lillooet District, British Columbia.

*unalaschcensis* (Gmelin).

Type locality.—Unalaska?

Range.—Alaska Peninsula, Shumagin Islands, and Unalaska Island.

*insularis* Ridgway.

Type locality.—Kadiak, Alaska.

Range.—Kadiak Island, Alaska.

*sinuosa* Grinnell.

Type locality.—Drier Bay, Knight Island, Prince William Sound, Alaska.

Range.—Prince William Sound region (both the islands and the mainland), Middleton Island, and the Kenai Peninsula, Alaska.

*anneotens* Ridgway.

Type locality.—Yakutat, Alaska.

Range.—Coast of Alaska in the Yakutat Bay region; probably extends north-westwardly nearly to the eastern edge of Prince William Sound, south-eastwardly about to Cross Sound.

*townsendi* (Audubon).

Type locality.—Columbia River, Oregon.

Range.—Coast region of southern Alaska, on islands and mainland, from Glacier Bay and Lynn Canal south to Forrester Island; also on the Queen Charlotte Islands, British Columbia.

*fuliginosa* Ridgway.

Type locality.—Neah Bay, Clallam County, Washington.

Range.—“from extreme northwestern Washington and Vancouver Island northward on the mainland only, at least to the Stikine River. On the latter stream it extends inland about a hundred miles, following the course of the river. Its extension inland elsewhere is unknown to me.” (Swarth, 1922, p. 263.)

*schistacca* Baird.

Type locality.—“South Fork of Platt River, about 25 miles east of north-eastern corner of Colorado, Nebraska.” A. O. U. Check-list, 1910, p. 277.) It is improbable that this bird was breeding at the place where it was taken.

Range.—The summer habitat is principally in the high mountains of the Great Basin region, north into Alberta, south into Nevada and east probably to eastern Wyoming.

*fulva* Swarth.

Type locality.—Sugar Hill (5,000 feet), Warner Mountains, Modoc County, California.

Range.—Extreme northeastern corner of California, in the mountains of Modoc and Lassen counties; north into central Oregon; east of the Cascades. The northernmost specimen at hand is from Warmspring, Crook County, the easternmost from Burns, Harney County.

*megarrhynchus* Baird.

Type locality.—Fort Tejon, Kern County, California.

Range.—Summer home unknown.

*brevicauda* Mailliard.

Type locality.—One-half mile south of South Yolla Bolly Mountain in Trinity County, California.

Range.—There are breeding birds at hand from South Yolla Bolly Mountain, which lies at the junction of Trinity, Tehama, and Mendocino counties, from Snow Mountain, in the northwestern corner of Colusa County, and also one juvenal from Mount Sanhedrin, in northeastern Mendocino County.

*canescens* Swarth.

Type locality.—Wyman Creek at 8,250 feet altitude, east slope of White Mountains, Inyo County, California.

Range.—Apparently confined to the White Mountains in Inyo and Mono counties, California.

*monoensis* Grinnell and Storer.

Type locality.—Mono Lake Post Office, altitude 6,500 feet, Mono County, California.

Range.—East slope of the Sierra Nevada in the vicinity of Mono Lake; possibly also in the Panamint Mountains.

*mariposae* Swarth.

Type locality.—Ridge at 7,000 feet, near Chinquapin, Yosemite Park, California.

Range.—Canadian and high Transition zones in the northern and central Sierra Nevada. Breeding stations represented by specimens at hand range from central Siskiyou County (head of Little Shasta River) at the north, south at least to the Yosemite region on the west slope of the Sierras, to Kearsage Pass on the east slope.

*stephensi* Anthony.

Type locality.—San Jacinto Mountains, California, at 8,000 feet.

Range.—Upper Transition and Canadian zones in the southern Sierra Nevada and the Sierras of southern California. There are several isolated tracts occupied by this subspecies, namely: in the Sierra Nevada from Hume and Horse Corral Meadow, Fresno County, south through Tulare County; on the summit of Mount Pinos, Ventura County; in the San Gabriel Mountains, San Bernardino Mountains, Los Angeles County; the San Bernardino Mountains, San Bernardino County; and the San Jacinto Mountains, Riverside County.

NATURAL HISTORY OF *PASSERELLA ILIACA*

|                                   |                                       |
|-----------------------------------|---------------------------------------|
| Name                              | Pre-nesting activity                  |
| Distribution                      | Food of adults in summer              |
| Habits                            | Territory                             |
| Winter habits                     | Voice                                 |
| Food                              | The nest                              |
| Seasonal range                    | Eggs                                  |
| Winter dangers                    | Incubation period                     |
| Habitats                          | Nesting dangers                       |
| Voice                             | Hatching                              |
| Association with other subspecies | Young                                 |
| Association with other birds      | Food and method of feeding            |
| Migration                         | Parental care                         |
| Method                            | Nest-leaving                          |
| Food habits and habitats          | Care and training after nest-leaving. |
| Association with other birds      | Second broods                         |
| Voice                             | Habits during moulting period         |
| Nesting                           | Fall migration                        |
| Summer habitat                    | Summary and discussion                |

## NATURAL HISTORY OF PASSERELLA ILIACA

The study of the internal structure of fox sparrows had not progressed far until it became evident that before an attempt could be made to interpret many of the features of variation that were encountered it would be necessary also to make a study of the natural history of the species. Accordingly, the scope of the proposed study was enlarged to include the natural history of the fox sparrow and since there is no adequate published account of the life-history of the species, the material has been organized to form a part of this report.

The material upon which this account is based was obtained from the following sources: (1) published works (chiefly local lists) which contain matter dealing with this species, (2) field notes and other material in the California Museum of Vertebrate Zoology, and (3) the field experience of the writer. An effort has been made to include under each heading enough examples to show the normal range of habits but at the same time to avoid needless repetition of facts.

Since one of the chief reasons for making this phase of the study was to determine the nature and amount of geographic variation in habits, the plan of presentation indicated by the outline (p. 266) was chosen. The annual cycle of activity has been divided into major divisions, each of which is dominated by some particularly important type of behavior. Each of these has been further subdivided and then under each subtopic the subspecies are taken up in the same sequence as in other parts of this report. In this way, it is hoped, geographically contrasted traits of behavior will be made more apparent than would be the case if each subspecies, in turn, were discussed fully. In other words, an attempt is made to present the facts in the form of a comparative study. This form of presentation makes it necessary to discuss, for example, food habits in four different places; but such a procedure is desirable if the influence of season is to be separated from the influence of geography.

## NAME

Eaton (1914, p. 321) gives this information concerning the derivation of the scientific name of the fox sparrow, "passerella, diminutive form of *passer*, sparrow; *iliaca*, prelinnean specific name of the Red-wing, from Gr. a thrush; perhaps from a superficial resemblance to a thrush."

Vernacular names given by Townsend and Allen (1907, p. 402) as applying to this species are "Fox Sparrow; 'Russingel'; 'Red Singer'; 'Red Thrush' (Stearns)."

#### DISTRIBUTION

The summer ranges of the races of the fox sparrow so far recognized have already been given (p. 264). In winter the range of the species is largely confined to the southern half of the United States and recently numerous specimens have been taken in Lower California, Mexico. So little has been learned about the winter distribution of the western races of fox sparrow since the publication of Swarth's revision (1920) that no attempt is here made to add to what he gives on that subject.

#### WINTER HABITS

##### FOOD

*iliaca*.—The most complete published account of the food of this species is that of Judd (1901, p. 88) which is based on the examination of 127 stomachs, collected from eastern states in winter months. Among the food items listed for this bird are: fruit of *Euonymus americana*, berries of *Juniperus virginiana*, poke berry, blueberries, elderberries, grapes, and blackberries. Most of the fruit seeds had been taken after the fruit had dried. Twenty-eight per cent of the food consisted of seeds of berries and of fruit skins. Buds of peach and pear trees were occasionally eaten by fox sparrows. Judd likens this bird to the cardinal in food habits because of the fondness of both for berry seeds and because both have powerful bills which enable them to feed on seeds that smaller billed species cannot crack.

*Other subspecies*.—At a feeding table kept by Mrs. Allen (1915, p. 82) fox sparrows ate both crumbs and seeds. It was observed that in this species the habit of scratching for food seemed so firmly fixed that the bird usually scratched among the crumbs before picking them up.

A bird that was watched by Mrs. Bailey (1902, p. 361) "took a little run forward and then kicked back with both feet, and if there were any diminutive hillocks back of him, leveled them, sending a shower of sand up behind him. Sometimes he used his bill to push a bit of earth aside."

Fox sparrows were feeding in December, 1924, in Tehama County, California, when snow covered the ground. The *Ceanothus cuneatus* bushes under which they fed held up the snow so that there was bare ground at the bases of the plants. The birds scratched so vigorously that litter was spread over the snow from six to eighteen inches from the edges of the bare ground (Grinnell, MS).

#### SEASONAL RANGE

A fox sparrow of a race which nests north of the United States was banded in Berkeley, California (Mrs. Allen, 1920, p. 16), on March 29, 1919. This bird stayed in the vicinity until April 21 when it left. The same individual reappeared at the feeding station on November 3 of the following fall.

#### WINTER DANGERS

*iliaca*.—In commenting upon the scarcity of fox sparrows in the Cambridge region in the years following the winter of 1894–95, Brewster (1906, p. 288) stated that, during that winter, they died by thousands from cold and starvation in the South Atlantic States. After five or six years, however, they began to increase rapidly and had regained their normal numbers by 1906.

#### HABITATS FREQUENTED

*iliaca*.—The farthest south occurrence in Louisiana is that of several in a "briery pasture on the edge of a wood on well drained land near New Orleans" (Kopman, 1915, p. 27).

*brevicauda*.—Mailliard (1924, p. 113) reported a few individuals of this race present in thick chemisal, ceanothus, and manzanita in Napa County, California. The same author (1912, p. 63) had previously reported their occurrence in Marin County, California, in winter, where he found them "in a sort of rocky mesa covered with dwarfed cypress, ceanothus and low, scrubby manzanita bushes, on the top of the range."

*Other subspecies*.—In the region of San Francisco Bay, where ten races of fox sparrows are known to occur, the associational preference, according to Grinnell and Wythe (1927, p. 122), is "pronounced for hillsides and canyon walls heavily clothed with chaparral, tangles of shrubbery and vines along stream courses, and, when the birds occur



in city parks and gardens, dense, low-growing shrubs and vines." These authors say that nothing is known about local occurrence or habits of these ten races by which any of them may be separately distinguished. They point out that the relative number of each subspecies varies from year to year and from place to place.

#### VOICE

*iliaca*.—Barrows (1912, p. 525) quotes this very satisfactory description of the song from C. J. Maynard: "These fine strains consist at first of three clear rather rapid notes, given with increasing emphasis, then a short pause ensues, and the remainder of the lay is poured forth more deliberately terminating with a well rounded note giving a finish to a sweet song."

In addition to the sharp chip note Goss (1891, p. 477) calls attention to a "soft Sparrow-like chip, or call note" and states that it "occasionally utters a few low, soft warbling notes" during the period of winter residence in Kansas.

Widmann (1896, p. 217) says that of the wintering birds in Missouri, the fox sparrow "deserves the highest praise for exhibiting the most undisturbable good humor all day long, and more than ever in the dusk of evening, his melodious voice goes through the leafless woods. It is not their full whistle which we hear in spring, but enough of it to show how happy they are and enough to make others happy too."

*Other subspecies*.—Keeler (1890, p. 117) in writing of wintering birds of this species in the vicinity of Berkeley, California, described the song as loud, rich, and varied and said that it was heard only on warm spring-like winter days. This observer noted also that the birds remained secluded while singing.

#### ASSOCIATION WITH OTHER SUBSPECIES

*sinuosa*.—Munro (1925, p. 158) found *sinuosa* to be the common wintering race on southern Vancouver Island, while *townsendi* was scarce and first appeared during a cold spell.

## ASSOCIATION WITH OTHER BIRDS

Mrs. Bailey (1902, p. 361) found fox sparrows in parks in San Francisco

with the white-crowned and golden-crowned sparrows. But though with the others, *Passerella* was not of them, and while the crowned sparrows were in goodly flocks he shoveled alone or possibly with a few comrades. When chased by a white-crown he gathered his feathers trimly about him and ran meekly into the bushes. He was evidently not as used to city life as they for when he came out in view it was with his red tail perked up, his wings close at his sides, and with a conscious air of appearing in public, and at the least alarm he would scud back to cover in nervous haste.

In contrast with this experience is that of Mrs. Allen (1915, p. 82) of Berkeley, California, who fed fox sparrows regularly at a "lunch-counter" and found them to be rather belligerent. At least they showed no more fear than did the other sparrows about coming to the porch railing for food.

Coues (1874, p. 161) remarked of the fox sparrow that "We do not find him mixing indiscriminately with the throng of Sparrows that accompany him in his journeyings and spend the winter with him. With a few select associates of his own kind, perhaps only two or three families that were reared together, he chooses his own retreat, and holds it against intrusion."

## MIGRATION

## METHOD

*iliaca*.—Cooke (1888, p. 211) has commented on the rapidity with which the fox sparrow migrates. He pointed out that it is not uncommon for the "... first, the bulk, and the last to be noted during the same week." In one instance, the spring of 1884, migration was prolonged because of a cold wave on January 1, which sent the species farther south than usual.

In Michigan, transient fox sparrows appear usually in two's and three's or in squads of about twelve, but sometimes in flocks of fifty or more (Barrows, 1912, p. 525). Brewster (1906, p. 288) has found as many as one hundred fox sparrows in a single flock and two hundred or three hundred in the course of a morning walk in the vicinity of Cambridge, Massachusetts. Experiences of Jones (1910, p. 98) in Ohio, indicate that fox sparrows are never found in flocks during migrations, but that they occur in scattered companies.

An account which Macoun (1909, p. 548) gives of the migration of this species through Toronto, suggests that its apparent scarcity there is due to the speed of migration in spring. Behavior of flocks is described as follows:

I have met with these birds in the middle of April when each bush contained several, many perched on the upper twigs singing the richest sparrow melody I know of. On visiting the locality the next morning at daybreak not a sign remained of our fleeting visitors; in the fall, their visit is of much longer duration, but on disturbing a small party of these birds while scratching the dead leaves for their food they will fly up into the nearest evergreen tree and remain perfectly motionless till the intruder has passed from view.

This experience is similar to that of Stone (1908, p. 241) in New Jersey who writes, "though common every year during their passage, they seem, some years, to reach us all together, as it were, and for a short time the thickets simply swarm with them. I noticed such a flight in March, 1906, near Tuckerton, when all the woods and fence rows seemed alive with Fox Sparrows."

Two hundred individuals were counted by one person at Nahant, Massachusetts, on April 10, 1907 (C. W. Townsend, 1920, p. 149). Whittle (1926, p. 498) gives it as his experience that this species arrives in migrations in small groups of eight to twelve birds which he thinks remain together until migration is resumed.

#### FOOD HABITS AND HABITATS FREQUENTED

*iliaca*.—Barrows (1912, p. 525) mentions a fox sparrow, examined by Professor E. H. King in Wisconsin, which had eaten fifty chinch bugs. Concerning the fox sparrow as a transient in Michigan, Barrows wrote that it "frequents the borders of woods and fields as well as the deep woods, but it spends almost all its time on the ground where it scratches continually among the leaves and rubbish often making noise enough to be heard at a long distance."

Brewster (1906, p. 288) writing of fox sparrows near Cambridge, said that they,

like Juncos, prefer upland to swampy places, although they are sometimes seen along the banks of brooks in thickets of alders and other bushes. Their favorite haunts in the Cambridge Region are dense second-growth woods, where the trees are largely pines, hemlocks, or other evergreens; rocky pastures plentifully sprinkled with Virginia junipers; and clusters or belts of bushes bordering roadsides and neglected weed-grown fields. They often appear in apple orchards and among ornamental evergreens in private grounds.

A fox sparrow, not in captivity, cited by Forbush (1908, p. 296), ate 103 seeds of *Panicum crusgalli* in 2 minutes and 47 seconds. Among the items identified by Eifrig (1910, p. 19) in the stomachs of three fox sparrows that were shot in Canada on April 22 and 24, are the following: Animal: beetle (*Aphodius*, weevil, and Elaterid larva); true bugs: lepidopterous larvae, millipeds, and spiders; vegetable: seeds of *Lithospermum*, *Panicum*, *Phleum pratense*, *Polygonum*, and *Rumex*.

The typical habitat of this bird in Ohio is given by Jones (1910, p. 98) as "brushy places either borders of woods, second growth, or even among the scattered brush cut from trees recently felled, especially if the cutting has left open spaces in the woods. It is also found in some numbers along hedge rows. . . . The fringing brush of the sand pit is a typical habitat, and it is there in rather more numbers than elsewhere." Jones found the bird feeding with towhees.

The experience of one observer (Florence A. Merriam, 1889, p. 175) in Washington, D. C., where this bird lingers for a short time, gives some insight into behavior during migration. She says,

They came to the boxes much more timidly than the other birds, slipping in quietly for a few mouthfuls, as if afraid of being seen. But they made themselves at home in the saplings on the edge of the woods right back of the house, singing in the sun quite fearlessly, even when I was walking about on the crust, staring at them through my glasses.

Stearns (1883, p. 277) wrote that while the bird is in New England it

haunts shrubbery and undergrowth of all kinds, pine and alder thickets, hedge-rows, and sometimes weedy fields, keeping much on the ground, where it is fond of rambling and scratching, much like a Thrasher or Towhee Bunting. . . . When disturbed in its retreats, it has a habit of mounting to some elevated or exposed perch, apparently to investigate the cause of the alarm, before determining to secrete itself in the recesses of the covert.

Surface (1913, p. 202) divided the food of fox sparrows into animal matter, 14 per cent, and vegetable matter, 86 per cent. He said, "The animal food is of little interest except that in April 20 per cent of all the food is millipeds (*Julus* group) and 10 per cent is ground beetles (Carabidae)."

*unalaschcensis*.—Individuals of this race that were taken by Dixon (MS) on April 18, 1920, in dense cactus (*Opuntia*) in a ravine on San Clemente Island, California, were exceedingly fat. One of these birds weighed fifty grams; more than any other individual of this species whose weight has been recorded.

## ASSOCIATION WITH OTHER BIRDS

*hiaca*.—Barrows (1912, p. 525) in Michigan, and Florence A. Merriam (1889, p. 175) in Washington, D. C., found this species associating with juncos, tree sparrows, and other sparrows during the migrations. Smith (1915, p. 50) reported it as transient in the Boston Mountains, Arkansas, where he found it with cardinals in thick brush-edged clearings.

## VOICE

*hiaca*.—Brewster (1906, p. 288) wrote that, strangely, they "sing most freely and with greatest spirit during stormy weather, especially when snow is falling."

The only note attributed to this species by Dawson (1903, p. 92) is a "Thrasher-like *chuck* of alarm" given as the bird speeds into cover. That writer gives the song as *Chee-hoo, her-weeoo, weoo, weoo, weoo*. In addition to this song he adds that the bird is more often heard singing, sometimes in chorus, in a subdued tone or "half-voice."

E. H. Eaton's impression of the song as this bird passes through New York is corroborative of the above statements. He says (1914, p. 322),

The song is usually delivered while the bird is perched on the limb of a tree from 10 to 40 feet from the ground. Sometimes it remains quietly perched for half an hour singing at intervals of a few seconds throughout the morning. Mr. Thayer has called attention to this sparrow's habit of singing in an undertone, sometimes for half an hour at a time, as if the bird were expressing day dreams of its summer home.

It has been suggested by C. W. Townsend (1920, p. 149) that since they often sing in cold, foggy, easterly weather they are then reminded of Labrador. Jones (1910, p. 98) says that they sing lustily on bright days.

Florence A. Merriam (1889, p. 175) compared the song of this species with that of the song sparrow and concluded that they were similar in arrangement of note but that of the fox sparrow "was richer, and had a plaintive cast." In commenting upon the song of this bird Judd (1901, p. 88) says, rather strangely, that "its song is utterly unsparrow-like, a unique performance that seems not in the least akin to bird music, but more like the soft tinkling of silver bells."

## NESTING

## SUMMER HABITAT

*iliaca*.—In Newfoundland, according to Griscom (1926, p. 679), the fox sparrow is more abundant than any other land bird. It is found (p. 665) with Lincoln and white-crowned sparrows in the stunted spruce. Young reported (Macoun, 1909, p. 547) that at Leeds, Ontario, he found this species frequenting second growth brush in old clearings. In the same work it is recorded, on authority of Turner, that at St. Michael, fox sparrows breed in "thickets of alder around the edges of the small lakes." In the Athabaska-Mackenzie region, Preble (1908, p. 446) found fox sparrows in "alder and willow thickets."

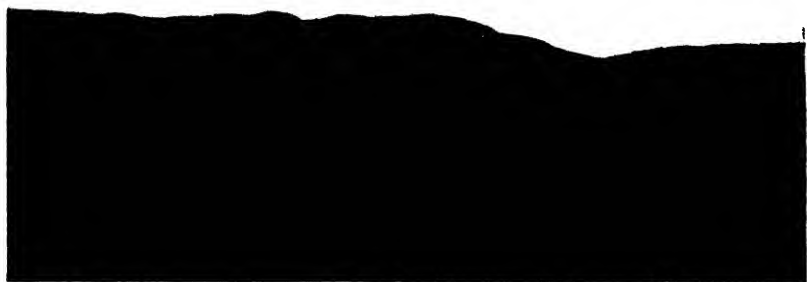


Fig. A. Summer habitat of *Passerella iliaca altivagans* on Nine-Mile Mountain near Hazelton, British Columbia. Fox sparrows nested in fir thickets above 5,000 feet; July 29, 1921. Mus. Vert. Zool., no. 3717.

The habitat of the race in Alaska was given by Dice (1920, p. 184) as "chiefly in the white spruces, paper birches, and willows along the streams, though one was noted in song in black spruces several hundred yards from other types of forest." Nelson (1887, p. 195) found the fox sparrow near St. Michaels after the tenth to fifteenth of May each summer "sharing with the Tree-sparrows the bushy shelter of the alder thickets on hillsides and sheltered ravines." It could be found "wherever a fair-sized alder patch occurs."

*altivagans*.—Racey (1926, p. 324) found this subspecies in British Columbia, in summer singing regularly from the clumps of stunted

fir trees. According to Riley (1912, p. 69) this bird is found in summer "around the small dense clumps of stunted spruces that grow in the protected hollows above timber line." Swarth (1924, p. 357) found this race breeding in tangles of alder and veratrum and a little above timber line on Nine-mile Mountain, British Columbia. Its surroundings resembled those of golden-crowned sparrows in the area.

*unalaschensis*.—On Little Kornushi Island, Bean (1882, p. 158) found this bird on top of a ridge, 1,200 feet above sea level. It was with snow buntings and pipits.

*sinuosa*.—Grinnell (1910, p. 406) records that this race, in the type locality, is most abundant as well as the most widely distributed land bird, being found from the beach to timber line, but chiefly in deciduous thickets.

*townsendi*.—Willett (1914, p. 87) noted that this race was partial to the smaller grass and brush covered islands in the vicinity of Sitka, Alaska. On Forrester Island, the same author (1915, p. 305) found this to be the most abundant land bird and found it occurring "in wooded localities everywhere." Later, he wrote (1922, p. 36) that this bird was more common on Forrester Island than at any other point in the southern end of the Alexander Archipelago.

*fuliginosa*.—This race was found by Swarth (1912, p. 62) on bush covered slopes and in willow thickets along the creek bottoms on Vancouver Island, but not in the dense forests below.

*schistacea*.—According to the observations of Bendire (1889, p. 113) this bird seems "to prefer the willows and rose thickets along the streams in the more open country, but is generally most abundant close to the foot-hills of the mountains." Saunders (1911, p. 44) wrote that in Montana fox sparrows prefer the "thickest and most impenetrable" willow thickets in the valleys.

This race was reported by Taylor (1912, p. 400) to be common in the Transition life zone, especially on the west slope of the main ridge of the Pine Forest Mountains, Nevada. The birds were found especially on the "rocky slopes, covered with chinquapin and quaking-aspen thickets, with a sparse intersprinkling of mountain mahogany and limber pine." Individuals were found with white-crowned sparrows and Macgillivray warblers in the vegetation about springs in the mountain meadows.

Walker (1917, p. 138) reported the occurrence of this subspecies in early May in central Oregon, in a thick growth of little pine seedlings, rather than their usual habitat, the brushy creek bottoms.

*fulva*.—Fox sparrows were present (Linsdale, MS) during the third week in June, 1926, in the shrubs and small pines on the slopes north of Butte Lake, Lassen County, California. The ground near here is rolling and there are no streams near. The lake is supplied by springs or seeps in the bottom. The habitat appeared to be similar to that in which *brevicauda* is found in Trinity County, California, but was drier and the birds were less numerous. The soil was a dark, slate-colored ash.

Three days were spent (Linsdale, MS) searching for this bird near the 5,000-foot line on Shields Creek, Modoc County, California, during the third week of June, 1926. The camp site was near the lower limit of pines along the creek. The slopes on either side of the creek were covered with sage-brush. Not one fox sparrow was found although an expedition from the California Museum of Vertebrate Zoology camped at the same location in the summer of 1910 and found fox sparrows to be fairly common.

During a ten-day period, beginning June 26, 1926, this bird was found but infrequently in the Warner Mountains (Linsdale, MS), at a 7,000-foot elevation near Eagle Peak, Modoc County, California. The slopes and valleys in this vicinity are rugged. Parts of the slopes were covered with sage-brush and other parts, near the sources of streams, had patches of aspens. On the higher slopes were pines. Fox sparrows were found chiefly among the aspens and bushes at the edges of rock slides although a few were seen along the streams. The adults were shy and hard to approach at this time. A few singing males were heard but they would not permit close approach.

*brevicauda*.—Birds of this subspecies were collected (Linsdale, MS) between May 4 and 26, 1926, in the vicinity of the divide twelve miles north of North Yolla Bolly Mountain, Trinity County, California. The camp was at 4,400 feet elevation. On the slope north of camp there were yellow pines and Douglas firs. On the north-facing slope just south of camp, Douglas fir was the dominant tree. A small stream near by ran toward the west. It was bordered by clumps of alder and willow and by several small clearings where ceanothus and small coniferous trees made more or less dense thickets. Several hundred acres of the land in the first valley north of camp had been burned over within recent years. Many burned stumps were standing. Most of the ground was covered with a dense thicket of brush, chiefly ceanothus. This valley sloped toward the west.



The sharp zonal contrast, apparent when the habitats and faunas of the two sides of the divide at this point were compared, was striking. The vegetation and animal life of the east-facing slope was characteristic of the Upper Sonoran life-zone. No higher zone animals or plants were found there. However, on the west-facing slope there existed a mixture of plants and animals of each of three zones. Canadian, Transition, and Upper Sonoran animals were found scattered wherever they could find suitable surroundings.



Fig. B. Summer habitat of *Passerella iliaca canescens* in White Mountains, Esmeralda County, Nevada, May 20, 1927. Photograph taken by Miss Annie M. Alexander.

All the fox sparrows that were collected in this vicinity were typical of the race *brevicauda*. When the work was started, May 5, fox sparrows were already on the ground and apparently established for the nesting season. Males, singing from the tops of ceanothus bushes or the tips of small pine trees, indicated the location of each pair of mated birds. In the burned-over area the fox sparrow was the most abundant bird species and it seemed to find conditions there more suitable for existence than elsewhere in the region since it was more numerous there than elsewhere. Not one fox sparrow was seen on the east side of the divide.

During a five-hour census through the open timber bordering the creek near camp on the morning of May 17, 11 fox sparrows were seen and 233 individuals of all other species.

*canescens*.—Field work was carried on (Linsdale, MS) in Esmeralda County, Nevada, and Mono County, California, during part of May, 1927, for the purpose of obtaining specimens of this form. The birds were present in small numbers along the streams above the 8,000-foot contour line. They were always near water and were usually found at the edges of springy places where there were thickets of



Fig. C. Close-up view of summer habitat of *Passerella iliaca canescens* in White Mountains, Mono County, California, May 25, 1927. Photograph taken by Miss Annie M. Alexander.

aspens and birches with dense ground covers of rose, gooseberry, or alder. The birds were found near snowdrifts where there was sufficient moisture and vegetation for their needs. Not a single individual was seen or heard on the nearby, dry, mountain sides which were covered with sage bushes and piñons. Tolmie warblers frequented the underbrush in the same places as the fox sparrows. The green-tailed towhee, often recorded as occurring in the same habitat as the fox sparrow, was numerous in this region in all the drier situations but only a few individuals were noted in surroundings favored by

fox sparrows and those individuals were not limited in their ranges so closely to the stream sides as were the fox sparrows.

*monoensis*.—This race was found by Dixon (MS) at Mono Lake, California, with hermit thrushes along the lake shore. In Alpine County, California, Hunt (MS) found *monoensis* commonest where there was manzanita undergrowth although it occurred all the way up from the sage flats into the fir belt of the mountains. It was never far from pines but ranged to their lower limit.

*mariposae*.—Mailliard (1921, p. 73), writing of this race in the vicinity of Lake Tahoe, California, records it as abundant in willow and aspen as well as in the ceanothus association. Taylor (1891, p. 123) writes of it as especially numerous on a "low brushy slope grown with young fir and pine trees."

In Little Onion Valley, California, this race frequents the thickets of willow and birch along the stream rather than the chinquapin patches on the hillsides (Swarth, MS).

Fox sparrows were collected and studied (Linsdale, MS) in the vicinity of Manzanita Lake, Shasta County, California, between June 5 and 12, 1926. Camp was made by the side of a small stream near the lake which is three and one-half miles northwest of the base of Mount Lassen. Just above the lake was a belt of chaparral about one mile in width where a species of manzanita (*Arctostaphylos*) was the dominant plant. At the upper edge of this belt were small patches of aspen. A dense, narrow belt of willows bordered the stream. On June 6 fox sparrows were numerous near the upper edge of the belt of manzanita. They were singing from the tops of the bushes and from two to four feet from the ground. As many as three or four were in sight at one time. Although the birds were found in numbers throughout the ensuing week it was hard to approach them because of the dense growth of bushes on the slope. A few fox sparrows were found in the willow thickets along the stream, even as far up as the base of Mount Lassen, but the greatest density of population was in the belt of manzanita. The birds in this vicinity were so nearly the color of the fine volcanic ash which makes up the top layer of soil that it was sometimes difficult to see a bird that had so fallen, after being shot, that only the feathers of the back were in sight.

From July 21 to 31, 1926, fox sparrows were studied (Linsdale, MS) in the neighborhood of Shaver Ranger Station, 5,300 feet, Fresno County, California. The station is surrounded by cut-over forest land that had grown up with dense thickets of ceanothus and other

chaparral plants. Nearly all the hunting was done on the upper part of the slope between the camp and the San Joaquin River. The San Joaquin River near this point runs in a narrow, deep canyon with walls nearly 3,000 feet in height. The lower portions of its walls have an Upper Sonoran fauna and flora which is replaced on the uppermost slopes by Transition animals and plants, although several species of birds were found which really belonged at a lower elevation. That is they had moved to higher altitudes after the close of their nesting seasons. Residents of this vicinity said that it is, as a rule,



Fig. D. Summer habitat of *Passerella iliaca stephensi* near Taylor Meadow, Tulare County, California. Left slope is north-facing and is covered with *Ceanothus cordulatus*. Mus. Vert. Zool., no. 565.

cooler in the "pocket" in which our camp was located than in any nearby locality of the same altitude. Except for the fact that it was noticeably colder here than it had been at Hume, also 5,300 feet high, during the previous week, the best evidence noted for low summer temperature of this vicinity was the presence of many fox sparrows, found chiefly in the thick clumps of ceanothus. On account of the extremely dry summer season there was a scarcity of water in the mountains so that the birds may have congregated in this valley in search of water. They came to drink at small seepy and wet places.

*stephensi*.—The habitat of this race in the San Jacinto area, California, was found (Grinnell and Swarth, 1913, p. 281) to be nearly coextensive with the distribution of the chinquapin (*Castanopsis*

*sempervirens*). Grinnell (1905, p. 388) reported it on Mount Pinos as occurring in the "rank growth of gooseberry bushes and other vegetation about springs and swales, particularly on the shaded north side among the firs." The same author (1908, p. 99) recorded the habitat of this bird in the San Bernardino Mountains as similar to that in the San Jacinto area.

Fox sparrows were collected (Linsdale, MS) in the vicinity of Hume, Fresno County, California, between July 13 and 20, 1926. Our camp was near a sawmill location at which an artificial lake had been constructed. The surrounding slopes were originally covered with large trees but since the recent clearing for lumber there has grown up a dense cover of sprouts and shrubs. Along the streams were small flats up to fifty yards in width on which grew dense thickets of willows. This bird was found in the brushy, cut-over land and along the streams.

#### PRE-NESTING ACTIVITY

*schistacea*.—Bendire (1889, p. 113) gives an account of the activity of this bird just after its arrival at Camp Harney, Grant County, Oregon, from which the following is quoted:

Here I found them quite tame and unsuspicious, and I have often seen them hopping around amongst the fowls and feeding with them. They usually arrived in that vicinity about the last week in March or the first week in April, and were amongst the earliest summer visitors to make their appearance. The greater part of the day was spent by them on the ground, scratching amongst the manure heaps or fallen leaves, searching for larvae, small worms, insects, grain, and seeds of different kinds. Like the other forms they are quite terrestrial in their habits.

#### FOOD OF ADULTS IN SUMMER

*brevicauda*.—Attempts to trap fox sparrows, by the use of seed for bait, were made by Mr. J. Mailliard (Linsdale, MS) in the Yolla Bolly Mountains in the early summer of 1926. His failure indicated that the birds fed almost exclusively on animal matter. Although the birds were common in the neighborhood none entered the baited traps. On May 21, 1926, in this same vicinity, two were seen to fly into the air, repeatedly, from stumps in a recently burned area and to catch successfully, each time, a passing insect.

*cancscens*.—Stomachs of ten fox sparrows that were killed at 8,200 feet altitude on Chiatovich Creek, Esmeralda County, Nevada, were

saved and were sent to the United States Bureau of Biological Survey for detailed examination. The report of C. C. Sperry of the Division of Food Habits Research is as follows:

No. 177438 Biol. Surv. (1945 J. L.), male, May 13, 1927; condition of stomach, full; percentage of animal matter 100; contents, fragments of a Carabid and of a weevil (*Panscopus* sp.), trace; 8 small *Aphodius alternatus*, 10%; spider fragments, 1%; remains of at least 10 *Camponotus* sp., 8 *Formica fusca*, and 13 *Myrmica rubra* (incl. *M. r. brevinodis*), 89%.

No. 177439 Biol. Surv. (1946 J. L.), male, May 13, 1927; condition of stomach full; percentage of animal matter 97, of vegetable 3, of gravel, etc., 2; contents, 1 weevil (*Panscopus* sp.), 2%; 1 *Cytilus sericeus*, 2%; 1 small Scarabaeid (like in 177441), 1%; bits of caterpillar, 1%; fragments of a fly pupa (*Fannia* sp.), 3%; 1 *Leptothorax* sp., 27 *Formica fusca*, and 34 *Myrmica rubra* (incl. both *brevinodis* and *scabrinodis*), 88% fragments of several small bivalves and of a spider, trace; 3 seeds of *Carex* sp. and fragments of 2 seeds of *Rubus* sp., 3%.

No. 177440 Biol. Surv. (1947 J. L.), male, May 13, 1927; condition of stomach, one-half full; percentage of animal matter 99, of vegetable 1, of gravel, etc., 10; contents, fragments of a weevil (*Panscopus* sp.), 2%; fragments of a Dipterous larva 1%; fragments of several small bivalve mollusks, 6%; 12 *Formica fusca* and 15 *Myrmica rubra* (incl. *M. r. brevinodis*), 90%; 2 seeds of *Carex* sp., 1%.

No. 177441 Biol. Surv. (1948 J. L.), male, May 13, 1927; condition of stomach, full; percentage of animal matter 100, of gravel, etc., 15; contents, 1 *Aphodius alternatus* and 2 other Scarabaeids, 4%; Diptera; 11 larvae and several pupae of Tipulidae, 60%; 13 *Formica fusca*, 9 *Myrmica rubra* (incl. *M. r. brevinodis*) and 1 *Leptothorax* sp., 32%; fragments of 2 small *Enochrus* sp., a caterpillar, a millipede, and a spider, trace.

No. 177442 Biol. Surv. (1949 J. L.), male, May 13, 1927; condition of stomach, full; percentage of animal matter 100, of vegetable, trace, of gravel, etc., 6; contents, fragments of a Tenebrionid, 1% and of 2 Staphylinids, trace; Weevils, 1 Ceutorhynchid and several Otiorhynchids (mostly *Goederces* ? sp.), 14%; Diptera: remains of a puparium and of Tipulid larvae, 3%; 26 *Formica fusca* and 19 *Myrmica rubra* (incl. *M. r. brevinodis*), 80%; fragments of small snails and bivalves 2%; 2 scale insects (like in 177443), trace; fragments of a spider and 2 seeds of *Carex* sp., trace.

No. 177443 Biol. Surv. (1950 J. L.), female, May 13, 1927; condition of stomach, one-half full; percentage of animal matter 90, of vegetable 10, of gravel, etc., 40; contents, 1 *Enochrus* sp., trace; 2 *Aphodius alternatus*, 10%; Diptera: remains of a puparium and Tipulid larva, 25%; Ants: 1 *Camponotus* sp., 6 *Formica fusca* and 3 *Myrmica rubra brevinodis*, 40%; 3 scale insects, trace; fragments of small bivalves, 15%; 1 *Carex* seed, trace; unidentified vegetable material, 10%.

No. 177444 Biol. Surv. (1951 J. L.), female, May 14, 1927; condition of stomach, full; percentage of animal matter 100, of vegetable, trace, of gravel, etc., trace; contents, at least 16 *Aphodius alternatus*, 20%; fragments of 6 *Sitona hispidulus*, 18%; 3 *Saprinus* sp., 3%; 5 *Cytilus sericeus*, 12%; 1 Stratiomyid larva and 1 puparium and an adult of *Helina* sp., 2%; 8 *Formica fusca* and 20 *Myrmica rubra* (incl. *M. r. brevinodis*), 45%; fragments of small bivalves, trace; fragment of seed of *Diodia* sp., trace.

No. 177445 Biol. Surv. (1952 J. L.), female, May 14, 1927; condition of stomach, full; percentage of animal matter 100, of vegetable, trace, of gravel, etc.,

10; contents, fragments of a Staphylinid, trace; 4 *Aphodius alternatus*, 6%; remains of several Tipulid larvae, 4%; Ants: 29 *Myrmica rubra* (incl. *M. r. brevinodis*), 4 *Formica fusca*, and 1 *Camponotus* sp., 90% fragments of 3 seeds of *Carex* sp., trace.

No. 177446 Biol. Surv. (1953 J. L.), female, May 14, 1927; condition of stomach, full; percentage of animal matter 100, of vegetable, trace, of gravel, etc., 1; contents, 7 *Aphodius alternatus*, 8%; 2 Staphylinids, 1%; Elateridae fragments, 3%; 7 *Cantharis* sp., 30%; 1 *Panscopus* sp., 1 Otiiorhynchid and 1 *Ceutorhynchus decipiens*, 4%; 1 *Enochrus* sp. and a Carabid larva, trace; 5 *Camponotus* sp., 19 *Myrmica rubra* (incl. *M. r. brevinodis*) and Hymenoptera fragments, 54%; fragments of an Anthomyid and a caterpillar, trace; spider fragments and 1 seed of *Potentilla* sp., trace.

TABLE 1  
SUMMARY OF FOOD OF ADULT *canescens* IN MAY

| No.           | Sex | Coleoptera | Hymenoptera | Diptera      | Mollusca | Spiders | Vegetable |
|---------------|-----|------------|-------------|--------------|----------|---------|-----------|
|               |     | %          | %           | %            | %        | %       | %         |
| 177438        | ♂   | 10         | 89          | .....        | .....    | 1       | .....     |
| 177439        | ♂   | 5          | 88          | (Lepid. 1) 3 | .....    | .....   | 3         |
| 177440        | ♂   | 2          | 90          | 1            | 6        | .....   | 1         |
| 177441        | ♂   | 8          | 32          | 60           | .....    | .....   | .....     |
| 177442        | ♂   | 15         | 80          | 3            | 2        | .....   | .....     |
| 177443        | ♀   | 10         | 40          | 25           | 15       | .....   | 10        |
| 177444        | ♀   | 53         | 45          | 2            | .....    | .....   | .....     |
| 177445        | ♀   | 6          | 90          | 4            | .....    | .....   | .....     |
| 177446        | ♀   | 46         | 54          | .....        | .....    | .....   | .....     |
| 177447        | ♂   | 2          | 98          | .....        | .....    | .....   | .....     |
| Average ..... |     | 15.7       | 70.8        | 9.9          | 2.3      | .1      | 1.4       |

*mariposae*.—Stomachs of two birds, taken in April, that were examined by Bryant (1911, p. 203) were filled almost completely with weed seeds. The only animal food in them consisted of parts of two ground beetles.

#### TERRITORY

*iliaca*.—Farley is cited by Taverner (1919, p. 257) as authority for the statement that in some places in Alberta as many as a dozen pairs breed on each square mile and that in such places their song is the commonest of any bird.

*schistacea*.—Tolerance for other species is indicated by W. P. Taylor's (1912, p. 400) observation of one singing in an aspen tree in which at the same time two black-headed grosbeaks were singing.

*mariposae*.—Two noisy pairs were observed at Mono Meadow on June 20. A male was belligerent and drove a western tanager and a Wright flycatcher from its territory (Grinnell, MS). The same

observer noted a singing male 125 feet above *Ceanothus* where it had gone to catch the first sun rays in the morning. A count of breeding birds on a small area near Mineral, California, showed six pairs of this race on six and one-half acres (Grinnell, MS).

#### VOICE

*iliaca*.—The song of this race in summer in Alaska was syllabified by Dice (1920, p. 184) in this way, "*Ee-chee, weer-r-r-a-chr-r-r-ree*." At the same time he gave the call-note as "a sharp *tchip*." According to Nelson (1887, p. 195) the song, in Alaska, was "*pew-e-e-dudy-jew*" and it was given by the males from the roof of the highest building. Osgood (1909, p. 41) observed that this species, along the Yukon, "often sings at night, mingling its melody with that of the thrushes."

On one of the Magdalen Islands, in July, 1879, Goss (1891, p. 477) heard the males singing, "almost constantly, from early morn till late at night." In Newfoundland (Arnold, 1912, p. 74), this race sings at all hours of the day and at times at sunset.

A good account of the song and calls of this species in Labrador has been given by Townsend and Allen (1907, p. 402) from which the following is quoted:

The song seemed richer and fuller than the best song given by this species during the spring migration in Massachusetts. Its clear flute-like notes are somewhat ventriloquial in character, and as the bird sings generally from a concealed perch inside of a spruce or fir tree a foot or two from the top, it is often difficult to find the performer. We have written down the song very inadequately in words thus: *cher-ee, hear-her, hear-her, tellit* or *to-whip, towhee, oh-uh-ee buzz tellit*, the last note short and faint and the main stress on the second and third bars.

The long drawn call note *stssp* so commonly heard in Massachusetts during the migrations, was rarely heard in Labrador. A sharp *ohip chip* was occasionally emitted, and the bird when disturbed sometimes gave the usual alarm note, a loud *smack*, richer than that of the Junco and more like that of the Brown Thrasher. One individual who was *smacking* in a fir tree emitted faint sneezy notes with motions of swallowing between the *smacks*.

*altivagans*.—Swarth (1924, p. 357) says that, although this bird was "constantly heard singing" in British Columbia, it was "so shy generally as to avoid observation."

*sinuosa*.—Grinnell (1910, p. 407) commented that the song of this race is heard in all kinds of weather and at all hours in summer.

*fuliginosa*.—Swarth (1912, p. 62) writing of singing birds on Vancouver Island wrote that "They were very shy and clung to the thickets of dense underbrush, so that it was difficult to get sight of



one. Singing birds were usually perched on a projecting branch, about the center of an impenetrable thicket of salmon berry or alder, into which they plunged at the first intimation of danger."

*schistacea*.—Concerning the song of this fox sparrow Bendire (1889, p. 113) wrote:

While the female is covering her eggs, the male may frequently be heard giving vent to his nuptial song, in the early morning and just before sundown. His lay, however, is rather weak and of small compass, very much resembling that of *Melospiza fasciata* [*melodia*] *montana*. He delivers it while perched on some small twig, overlooking the thicket in which the nest is placed and generally close to it. Their usual call note is a repeated *tzip*, *tzip*.

Ridgway (1878, p. 875) pointed out that this species resembles the song sparrow in habits except for being more terrestrial. He found their songs so nearly alike as to be difficult to distinguish when both species were singing together. This race was characterized as being a "very ordinary songster" in contrast to another [*mariposae*] which was called "one of the most remarkable songsters."

It has been definitely established by Saunders (1910, p. 80) that the female fox sparrow sings. The following is his account of his observations of a pair in a willow thicket near Bozeman, Montana, on April 17, 1909:

At first I believed, from their action that the birds were mating, but later, when I noticed that both birds sang alternately, I decided that they must be rival males. The songs were very similar in every way except that one was somewhat weaker than the other. I finally secured the bird with the weaker song and was much surprised when, on later examination, it proved to be a female.

The same author (1911) says that the song period for this bird ceases July 10, after which he has no records of the occurrence of the species.

*mariposae*.—Mailliard (1921) observed that "sometimes, while near the nest, the male breaks into song, not only when standing on the ground but when he is scratching or hopping about in the brush as well." H. R. Taylor (1891, p. 123) records their singing at dusk "during a shower of rain."

A male that was watched by Storer (MS) was singing in the top of a nine-foot spruce at intervals of eight to twenty seconds. The bird threw its head upward and opened its bill widely. The song was of two types: one with a trill and one without it. Sidewise movement of the tail was noted in one bird.

A singing male that was watched by Grinnell (MS) spent four-fifths of its time singing from a perch six feet from the ground half-

way up a clump of black oaks, which were barely coming into leaf. The singing post was fifty feet from the nest. Occasionally the bird went to another post in the chaparral and once mounted forty feet on a bare lower limb of a sugar pine to sing.

#### THE NEST

*Alaska*.—Arnold (1912, p. 74) described nests he found in Newfoundland, as "made of grass, moss, rootlets, caribou hair, etc., and are usually placed on the ground at the foot of a small spruce, sometimes 2 to 5 feet up in the branches of spruce trees." One nest was found by Brown (1912, p. 96) as high as twenty feet from the ground. Another nest was three feet from the ground and between the trunk and loose bark of a large pine tree. Still other nests were found in the roots of upturned stumps. Bendire (1889, p. 108) described a nest collected by C. Drexler at Moose Factory, June 2, 1860, which, "containing four fresh eggs, was placed in a pine bush, two feet up and well concealed from view. On the outside this nest is five inches wide, by three inches deep, inside three inches wide by two inches in depth." Most of the fox sparrows' nests found in northern Canada, by MacFarlane (1891, p. 443) were in trees and resembled those of the gray-cheeked thrush. A few that he found on the ground were "composed of coarse dry grass, lined with some of a finer quality, a few deer hairs, and a sprinkling of fresh moss."

Nesting habits of fox sparrows on the Magdalen Islands have been well reported on by Philipp (1925, p. 77). The following account is quoted from his work.

The nests are large and bulky, though exceptionally well built, and in spite of their size are very difficult to find, so carefully are they concealed. There are two distinct nesting situations. One, that most commonly adopted, is on the ground, either in a wet bog or on a dry hillside, under a thick mossy spruce-root or a brush pile, and usually in a very thick place. The other situation is in a spruce bush, usually at a low elevation, though I have seen nests fifteen feet from the ground.

In the early summer of 1923, because of snow on the ground, the birds were forced to nest in trees.

These Sparrow nests are made of a varied collection of materials. One before me that is typical has an outer wall of spruce twigs and Sphagnum moss, with a considerable amount of deadwood chips and coarse grass. The inner lining is of fine dried grass, and the cavity is well cupped and plentifully lined with cow hair.

*sinuosa*.—A nest that was found July 9, on Montague Island, Alaska, was described (Grinnell, 1910, p. 407) as "composed externally of a mixture of green moss, skeletonized leaves and coarse grasses, while in strong contrast there is internally a thick lining of fine, round grass stems."

*townsendi*.—A nest from Admiralty Island was described (Grinnell, 1909, p. 232) as "a bulky structure, 120 mm. high by 160 mm. across, the walls being very thick. The inner cavity is 70 mm. across by 50 deep. The main part of the nest is a matted mass of dead twigs, leaves, moss, and weathered grasses and the lining is of finely frayed out grasses mixed with duck feathers."

The location of some nests is given by Willett (1915, p. 305) as variable "some being ten or twelve feet up in trees, some in brush thickets and on fallen logs and others on the ground."

*schistacea*.—Bendire (1889) has given a complete account of the nests of this bird from which the following is taken :

The nests of this form are bulky, but exceedingly well constructed affairs. The material composing the outer body is used at least in a very damp, if not in a positively wet state. It is thoroughly welded together in this condition, forming when dry a compact, solid structure which will retain its shape perfectly. They are rather deep for the size of the bird, and cup-shaped. The finer finishing touches are attended to by the female, which fits the material used as the inner lining of the nest carefully in its place. As a rule two or three days are consumed in the construction of a nest, but I have positive evidence, in one instance at least, that a pair of these birds built an entirely new nest, and did it well too, between sunrise and sunset of the same day, and an egg was deposited in it that evening.

A typical nest he describes as

outwardly constructed of various coarse plant fibres, willow bark, and marsh grass, and lined with fine grass tops taken from a species of rye grass. The outside of the nest is four and a half inches across by four inches deep, the inner diameter is two and a half inches, the depth two inches. About one-third of the nests examined by me (some fifty in number) were lined inside with more or less horse-hair, and a couple, in addition, with feathers.

Concerning the nest site Bendire continues :

The Slate-colored Sparrow, according to my observations, prefers to nest in willow thickets, next in dense wild rose bushes, and occasionally in a bunch of tall rye grass, but always close to water. The nests are generally placed some little distance from the ground, rarely at a greater height than three feet, and are invariably well hidden. But a single instance came under my observation where the nest was placed directly on the ground; in this case it was hidden by an overhanging bunch of some species of swamp grass.

*fulva*.—Bendire (1889, p. 111) found the nests of this fox sparrow in *Kalmia* thickets, service-berry and willow bushes, and in thick, scrubby evergreens. The nests were always well hidden and were from a few inches to several feet from the ground. One nest was composed externally of coarse plant fibers and dry willow bark, and was lined with fine grasses and a few horsehairs.

*mariposae*.—Of fourteen nests found by Mailliard (1921, p. 73) six were on the ground. Three of those above ground were in *Ceanothus* the site varying from the edge of a thicket to the interior. One nest

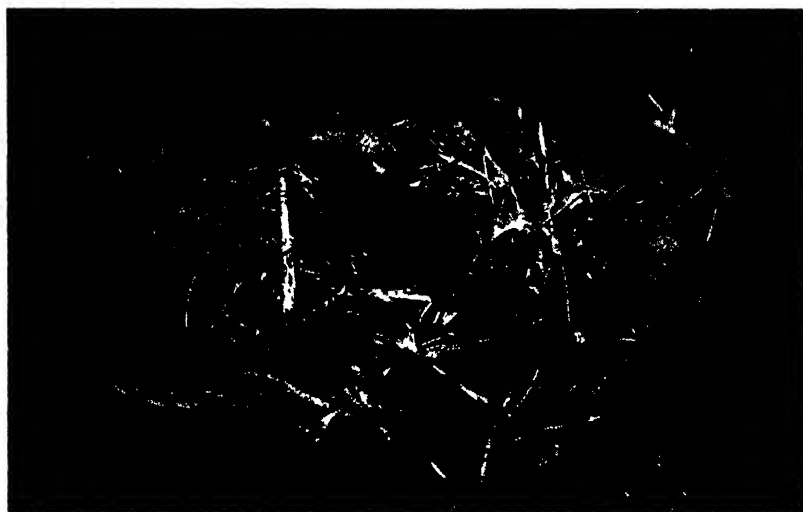


Fig. E. Yosemite fox sparrow (*Passerella iliaca mariposae*) at nest, Battle Creek Meadows, 4,800 feet, Tehama County, California, June 17, 1925. Mus. Vert. Zool., no. 4646.

was two feet above the ground in a crotch formed by a two-inch branch and a large willow. Another was on a mass of dead branches and debris under a clump of willows and two feet from the ground. One was on a dead branch of an aspen and was three feet above a small stream. That writer comments that all the nests followed a well established form of construction. He describes them as follows:

In all instances the nest proper was composed of combinations of shreds of old bark, small dead twigs, old chips and chunks of wood and dead leaves. All of this material, more or less decayed and very light in weight, was used in varying proportions in the different nests, sometimes one or two of these constituents being omitted. The wall of one nest contained several chips of wood, the largest of which was five and one-half inches long by one and a quarter wide, and very thin, possibly a piece of berry basket. The lining of the nests was of finely shredded bark, dead rootlets, old dry grasses and sometimes horsehair.

In the above-mentioned account a nest-building bird is described which picked up twigs within a few yards of its nest and flew directly to it with them. It is concluded, there, that the female alone builds the nest.

A nest found near Chinquapin by Grinnell (MS) was made in the basal part of short coarse twigs, then had a layer of more closely laid pine needles with an inside layer of deer hair and a few long black mane or tail hairs of horses.

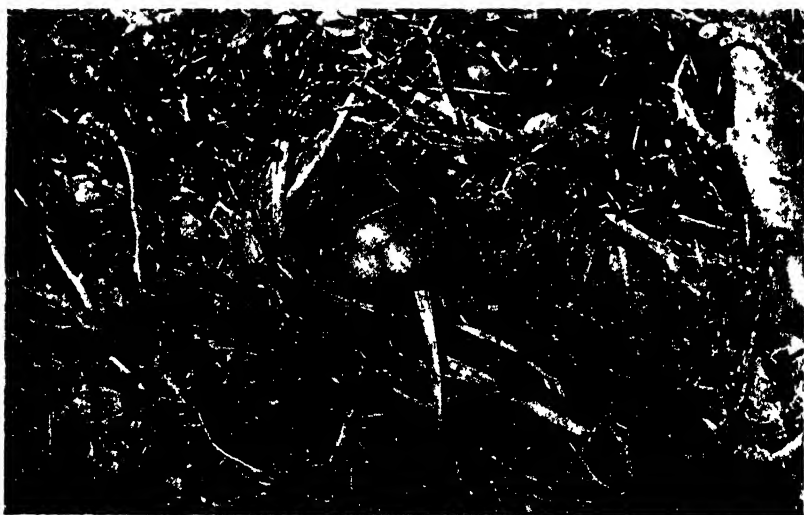


Fig. F. Nest and eggs of *Passerella iliaca mariposae*, Battle Creek Meadows, 4,800 feet, Tehama County, California, June 18, 1925. Mus. Vert. Zool., no. 4645.

*stephensi*.—Pierce (1921, p. 84) found nests of this race to be composed of coarse sticks and pine needles, with fine twigs and weed bark, lined with grass, weed bark, and sometimes mammal fur. The nests he found on the ground were less well made and contained more pine needles and leaves, rather than coarse sticks.

#### EGGS

*iliaca*.—Three is the typical number of eggs given by Arnold (1912, p. 74) and Brown (1911, p. 92; 1912, p. 96) for this subspecies in Newfoundland, although Brown (1912, p. 96) records one nest which contained five young.

Bendire (1889, p. 108) cites Sir John Richardson as authority for the statement that the eggs are five in number and adds that he thinks that four is the usual number and that five is rather exceptional. This author gives these measurements for a series of eggs:

|               |                 |
|---------------|-----------------|
| Maximum ..... | 25.4 × 17.3 mm. |
| Minimum ..... | 20 × 15 mm.     |
| Mean .....    | 20 × 16 mm.     |

According to MacFarlane (1891, p. 443) the number of eggs varies from four to five in the northern part of Canada.

Writing of this bird on Magdalen Islands, Philipp (1925, p. 77) says "The eggs are large and well marked, and the complement is usually three or four. A series of fifteen eggs shows: Largest,  $25 \times 18$  mm.; smallest,  $23 \times 17$  mm.; average,  $24 \times 17.5$  mm."

*sinuosa*.—A nest from Montague Island contained three eggs (Grinnell, 1910).

*townsendi*.—Grinnell (1909) comments, on a set of eggs from Admiralty Island, that they "resemble closely a common type of song sparrow's eggs."

Willet (1921, p. 36) examined fifty nests in six summers. The majority of the eggs were found between May 20 and June 20. Extreme dates were April 29, when one fresh egg was found, and July 9, when three eggs were found. That author (1920, p. 139) gives the usual complement of eggs for this bird as three, but in one summer season (1920) four out of seven nests found contained four eggs each.

*schistacca*.—Bendire (1889) says "The usual number of eggs laid by these birds is four, although three are not infrequently found. I found but two nests in fifty containing five eggs, the latter were evidently very uncommonly large sets." He gives these measurements for eggs:

|               |               |
|---------------|---------------|
| Maximum ..... | 24 × 17 mm.   |
| Minimum ..... | 18.8 × 15 mm. |
| Mean .....    | 22 × 16 mm.   |

*fulva*.—Bendire (1889) gives the usual number of eggs for *fulva* as three or four.

*mariposae*.—A completed set of eggs which contained only two eggs was reported by Barlow (1901, p. 172) from the vicinity of Lake Tahoe, California. H. R. Taylor (1891, p. 123) records several complete sets of three eggs and one of only two.

*stephensi*.—Hanna (1924, p. 150) has recorded the weights of five eggs of this subspecies as follows: average 3.43 grams, maximum 3.66 grams, minimum 3.14 grams.

Pierce (1921) records four nests of this bird with three eggs and one with two eggs.

## INCUBATION PERIOD

*iliaca*.—Philipp (1925, p. 77) has found that the female does most of the incubating and that the male spends most of his time singing to her, keeping it up "till late in the twilight."

*schistacea*.—Bendire (1889, p. 113) says that incubation "lasts from twelve to fourteen days; both sexes assist."

*mariposae*.—A bird which was flushed from a nest in the region of Lake Tahoe, California, ran quietly along the ground and disappeared (Barlow, 1901, p. 172).

Belding (1903, p. 79) reported a peculiar reaction of an incubating bird to disturbance. Because it seems so strange, the whole account is quoted here:

Many years ago I took a nest and four fresh eggs of the thick-billed sparrow [*mariposae*] from a bush of *Ceanothus cordulatus* and secreted it in a sparse growth of "mountain misery" (*Chamaebatia foliolosa*) forty or fifty feet from where I found it. In a hour or two I returned for the nest which I found but the eggs were gone. I happened to see one of them two or three feet from the nest in a line with its former site, and following that line I found them all. One was directly under the place from which I had taken it, one was nearly there, and the other was not more than twenty feet from it. I inferred that the parent birds had rolled them on the ground, which they could easily have done, as the course was free from any great obstacles, and was gradually descending.

Keyes (1905, p. 17) wrote, of an incubating bird, that it "was very tame and all but allowed me to touch her with my hand."

Mailliard (1921) concludes, that the female alone incubates, because of "the continual song of the male, from his favorite perch near the nest site, and the fact that the sitting bird, while feeding nearby, is not replaced by its mate."

An incubating parent that was disturbed by H. R. Taylor (1891, p. 123) flew excitedly near him and trailed in the grass to entice him away.

*stephensi*.—Pierce (1921, p. 84) concluded from observing this race that "the birds are very close sitters."

## NESTING DANGERS

*mariposae*.—Mailliard (1921) comments on the dangers to this bird during the incubation time as follows:

In spite of the startling amount of general destruction of eggs, young and nests of birds, presumably by chipmunks, predatory birds, snakes, etc., prevalent in the Lake Tahoe region, no nests of this fox sparrow were molested before the eggs were hatched. This was probably due to the facts (established by careful observation) that incubation commences with the laying of the first egg, and that the sitting bird never goes far from the nest.

Contrary to that experience is that of Ingersoll (1913, p. 84) in the region of Cisco, Placer County, California, from June 7 to July 7, 1912. A three and one-half inch snow fell on June 23. Of sixteen nests of this bird found within two miles of Cisco, two nests and sets of eggs were taken, two nests were emptied of eggs by children, one with two eggs abandoned before incubation commenced, one with four eggs destroyed by sheep feeding on foliage of bush, five nests with dead nestlings examined after the snow, four nests were emptied by jays, and "one nest with two piped eggs was discovered through the actions of a jay that had its feast interrupted."

## HATCHING

*iliaca*.—Macoun (1909, p. 547) records a nest with eggs as late as July 18, 1888, on Methye Portage in Canada, and Osgood (1909, p. 41) found just-hatched young near Circle on July 11. He took young, able to fly, on June 23.

## YOUNG

## FOOD AND METHOD OF FEEDING

*fulva*.—A female was shot (Linsdale, MS) on June 20, 1926, while gathering insect food, presumably for young birds in brush north of Butte Lake, Lassen County, California.

*mariposae*.—A female that was caring for two young in a nest at Battle Creek Meadows, Tehama County, California, fed them at intervals of from two to five minutes (Dixon, MS). The male brought food only twice. When the female approached the young with food she gave a low "throaty nest call" which was answered at once by a high pitched chipping of the nestlings. Most of the food brought



consisted of green measuring worms, half an inch long and small insects which were secured in warbler fashion from the green *Ceanothus* bushes within twenty-five feet of the nest. About one-fourth the food for the young was secured by scratching. The parent seemed to see the insects best when they were six to eleven inches away. Twice the parent picked off pieces of green plant (*Montia*) and fed them to the young. The male foraged farther from the nest than the female, going as far as fifty feet away. Several times he brought insects which he gave to the female which, in turn, gave them to the young birds.

#### PARENTAL CARE

*iliaca*.—Philipp (1925, p. 77) observed that both parents fed the young after hatching and that they kept the nest "scrupulously clean."

*mariposae*.—In a nest that was watched by Grinnell and Dixon (MS) the female brooded the young to shade them from the sun especially when the young began to hold their mouths open. She ate the excreta as they were voided by the young.

#### NEST-LEAVING

*mariposae*.—When young are nearly ready to leave the nest they will jump out and begin hopping away at even a slight disturbance. They go in different directions and are sometimes led away by the parents independently (Grinnell, MS). After the birds have once jumped out of the nest they will not stay in it even if they are replaced.

#### CARE AND TRAINING AFTER NEST-LEAVING

*iliaca*.—Brown (1921, p. 96) observed many young birds "skulking in the underbrush" during the first week of June. The birds, reported on by Philipp (1925, p. 77) stayed around the nest in family parties until quite well-grown.

*mariposae*.—In Yosemite Valley, California, on August 17 an adult and juvenile were watched by W. P. Taylor (MS) who thought that the adult exposed itself to distract attention from the young one. The young bird was giving a noticeably weak call note.

*stephensi*.—Taylor (MS) gives a call note of a juvenile which he heard in Tulare County, California, as "*tsip tsip sip sip so sip sipsip*."

## SECOND BROODS

*iliaca*.—Brown (1911, p. 92) considered the nests he found in the latter part of June in Newfoundland, to be second nestings. Goss (1891, p. 477) found young birds, nearly full grown, on the Magdalen Islands, in July and from the actions of the parents he thought they were preparing to rear a second brood. His opinion was based chiefly on the conspicuous song activity of the males. Philipp (1925, p. 77)



Fig. G. Young of *Passerella iliaca mariposae*. This shows the bird at the age when a slight disturbance will send it hurriedly from the nest. Chinquapin, Yosemite Park, California, June 13, 1915. Mus. Vert. Zool., no. 1643.

came to the same conclusion at the same locality because he found fresh eggs late in June in situations where he thought one brood had been successfully reared.

*townsendi*.—On Chicagof Island, Alaska, where this race was abundant full fledged young and old birds building were seen by Dixon on June 25 (Grinnell, 1909, p. 232). From observations made on Forrester Island, Alaska, Heath (1915, p. 27) concluded that this race raised two broods each year. Willett (1915, p. 305) from observations at the same place reached the same conclusion.

*schistacea*.—In Grant County, Oregon, Bendire (1889, p. 113) observed that, at least, some pairs reared two broods in a season.

*fulva*.—Bendire (1889, p. 111) thought that birds of this race reared only one brood in a season at Fort Klamath, Oregon. My observations on this race in Modoc County, California, indicate that in that locality only one brood is reared in a season.

#### POST-NESTING ACTIVITIES OF YOUNG AND ADULTS

*iliaca*.—Griscom (1926, p. 679) observed that in late summer in Newfoundland, family parties hunt along the beach, feeding upon the dead and drying fish on the ground around the villages.

*townsendi*.—Willett (1921, p. 36) has noted on Forrester Island, Alaska, that these birds move up the mountain sides in the latter part of August. They come down again in cool weather.

*fuliginosa*.—This race was observed near Victoria, Vancouver Island, by Macoun (1909, p. 552) who writes, "A marked peculiarity of this bird is its scraping among the leaves when feeding, just like a hen. While doing this it hops about with its tail elevated like a wren."

*mariposae*.—Fox sparrows were feeding on the *Amelanchier* berries, which were turning red but had not yet ripened, on July 26, in Tehama County, California (Grinnell, MS). Swarth (MS) was able to lure a few birds into the open by "squeaking" as late as September 2, but it took a great deal of time. At this time the birds were giving only fragments of their full song.

#### HABITS DURING MOULTING PERIOD

*iliaca*.—Grinnell observed this species, in the Kotzebue Sound region, just before its departure for the south. He described the birds (1901, p. 52) as "shy," it being almost impossible to chase them out of the brush. This contrasts with Nelson's (1887, p. 195) account of the birds along the coast of Norton Sound at that season when the "males renew their songs and are less shy than in the spring."

The following comments on moult and plumages of the fox sparrow (subspecies *iliaca*) are taken from the account by Dwight (1900, p. 206):

Juvenal plumage acquired no doubt by a complete post-natal moult. . . . First winter plumage acquired by a partial postjuvenal moult which involves the body plumage and wing coverts but not the rest of the wings nor the tail. . . . First nuptial plumage acquired by wear which produces slight changes. A few new feathers are usually acquired about the chin in March,

possibly the beginning of a more extensive moult. My last spring specimen is April 8th. . . . Adult winter plumage acquired by a complete postnuptial moult. Practically indistinguishable from first winter dress. . . . Adult nuptial plumage acquired by wear as in the young bird. Female.—The sexes are alike and the moults correspond although females average duller in color.

*altivagans*.—Swarth (1924, p. 357) found young birds "in process of change from juvenal to first winter plumage" flying about from July 22 to August 13, in the Skeena River region.

#### FALL MIGRATION

*iliaca*.—This species was found commonly by Grinnell (1900, p. 52) at Kotzebue Sound, Alaska, until August 23, when the birds abruptly disappeared. It was heard singing almost every hour of the day until the day of departure.

Osgood (1909, p. 41) saw "migrating or wandering" fox sparrows at the head of Seward Creek from August 30 to September 3.

On the Charity Islands, Lake Huron, Wood (1911, p. 103) saw fall migrating fox sparrows about a pond, feeding on the exposed mud flats. They flew into thick willow and rose bushes at the edge of the pond when they were disturbed. The birds "appeared to migrate alone." Chaney (1910, p. 276) recorded seeing one of these birds on a steamer in the middle of Lake Michigan on September 27.

*altivagans*.—Migrating individuals of this race were first seen by Swarth (1924, p. 357) in the Skeena River region on August 29.

*townsendi*.—Willett (1914, p. 87) recorded this subspecies as common in the vicinity of Sitka, Alaska, as late as early October.

*fuliginosa*.—This race was found migrating in unusual numbers by Mailliard in southern Humboldt County, California, in the fall of 1921. He wrote that (p. 51)

it was not unusual to see from half a dozen to twenty-five or thirty of them among the dead branches of a good sized bush after their curiosity had been excited by a succession of 'squeaks' on my part. . . . The thorn bush here bears quantities of small, round seeds about the size of, and somewhat resembling, the hemp seed used as a food for canary birds, and this food appeared to be what attracted such numbers of the sparrows to this locality.

## SUMMARY AND DISCUSSION

The fox sparrow, so named from the color of the eastern race, is best known in the United States as a winter visitant; for it is found in the more settled portions of the country only at that season. The food of this bird in winter consists almost entirely of vegetable material which it obtains by scratching under bushes and in weedy thickets. During the most severe winters the northern-most wintering birds suffer heavy losses from cold and starvation. Often several years are required for recovery to the normal population. Some of the western races have, in the California chaparral, a type of wintering habitat that differs considerably from anything available to the eastern bird. Although the number of individuals and the races represented vary, in general, from year to year, there is one recorded instance of an individual returning to the same spot for two consecutive winters. The song of this species in winter is fragmentary when compared with that in summer.

This species migrates in small groups which rest and feed in brushy places during the day. The migration flight of the whole species is so rapid that the birds are often considered rare in regions through which large numbers must pass. The migrating birds are found during the day in a great variety of places but they prefer dense growths of vegetation and moist places. The food at this season is composed of both vegetable (seeds) and animal matter but the proportion of animal matter is greatly increased over that in the winter months. During migrations the fox sparrow is found in the company of other fringilline species with somewhat similar choice of feeding ground. The birds often sing in the spring, even during stormy weather, which is normally encountered on the migration route at that season.

Under the head of summer habitat it seems reasonable to expect some expression of differential choice which may be correlated with change in geography. It is evident that not only is there a differential habitat choice through the range of the species but that, in general, the areas of uniform habitat correspond to the ranges of various subspecies. For example, in the schistacea group of subspecies the three smallest forms, in the Great Basin mountain ranges, are rather closely limited in summer to the narrow fringes of willow, aspen, and birch which grow along the streams on the dry mountain sides. Farther west, in the California mountains, the birds are found scattered through the dense growths of chaparral on the high slopes. In the

north where the climate is more moist the birds are found in various types of brushy vegetation in different localities, but everywhere the habitat is different from those of the southern races.

The available accounts of habitat preference in various parts of the species' range are too fragmentary to permit more definite statements as to the subspecific choice of summer surroundings, but they are sufficient to indicate with some degree of certainty that when they are better known the habitats of the races can be classified on a basis comparable with that on which the skins are studied.

It may be well at this point to indicate a relation which exists in California between fox sparrows and forest fires. When yellow pines have been cut or when fires occur so frequently as to kill these trees, the ground is soon covered with dense mats of the kinds of brush which are most suited to the needs of the fox sparrows of the region. Such a preference has probably existed on the part of the sparrows for a long time but within recent years, since occupation of the land by white men, the amount of suitable territory has been increased enormously by this artificial factor. As nearly as can be determined the fox sparrows have increased in a rate proportionate to the increase of new and suitable territory. To take advantage of this increase in area of suitable habitat necessitates an increase in rate of survival in the sparrows or else such a spread would result in diluting the whole population. Field observation indicates that in these newly occupied areas the density of population is even greater than it probably was under earlier conditions. May it not be possible that this tendency to respond quickly to new environmental opportunities has an intimate relation to the great capacity to vary which these birds exhibit? This clue may lead us to the discovery of many facts that would be of interest for their bearing on evolutionary problems.

The available evidence concerning food habits of fox sparrows supports the belief that in summer the food is approximately 98 per cent animal matter, of which nearly 95 per cent is insects. The food is obtained chiefly from the ground although some is taken from the leafy branches of low bushes and some is taken from the air, flycatcher style.

The songs of fox sparrows, considered from a geographic point of view, show tendencies to vary that may be correlated with differential choice of habitat and with structural differentiation. The species, as a whole, is especially noted for its highly developed vocal powers. There is, however, an easily distinguished gradation of volume and quality among the races of at least the *schistacea* group.

The song of the smaller races in the Great Basin resembles that of some song sparrows more than that of some of the closely related fox sparrows in the territory to the west.

The rather bulky nests of this bird are usually so well hidden as to be found with difficulty. They are placed in numerous types of situations although usually near the ground. There appears, from incomplete information, to be a tendency for birds in the northern parts of the range to place their nests higher than do those to the southward. This might be partly due to necessity since in the south most of the available nest sites are within a few inches of the ground. A great variety of material is used in the construction of the nests.

There is a considerable amount of individual variation in respect to color in the eggs of this species. The eggs are, in every way, strikingly similar to those of the song sparrow. Records are sufficiently numerous to show that in the northern part of the species' range four is the usual number of eggs and five are not uncommonly found. In the southern portion of the range three is the number most frequently found, and two are often recorded. There is considerable evidence that at least some of the northern races regularly rear two broods in a season while those farther south rear but one.

Concerning this question Thompson (1926, p. 269) writes that

it has recently been stated by English [1923] that resident tropical birds with nidicolous young (i.e., fed by the parents) tend to have smaller broods than species which nest in high latitudes. There is some evidence, indeed, that in the case of a single species larger clutches may be laid in the higher latitudes than in the lower latitudes of its breeding range. If this may be taken as related to the length of day available for the search for food, it indicates an advantage in spring migration from the Tropics to high latitudes which would not be served by, say, finding a temperate climate closer at hand at a suitable level on some tropical mountain range.

There is one other factor which might account to some extent for the larger clutches of eggs in the northern part of the range of this species. It is shown in another place that those birds which nest farthest north have the longest routes of migration. It is also known that many sorts of dangers beset migrating birds so that it is reasonable to infer that those birds which migrate a long distance would suffer a greater percentage of loss in numbers than would those which travel only a short distance. If this inference be correct, an increased rate of production among the northern birds would be required to maintain their normal numbers, or a decrease in that rate in the south if overproduction is to be avoided. Such a differential rate of reproduction is found among the fox sparrows. With this increased reproductive rate and increased elimination, presumably by selection, and

chiefly during periods of migration, an opportunity may be afforded for evolutionary changes to go on at a faster rate in the northern part than in the southern part of the range of the species.

Observers of this species agree that the female does most of the incubating while the male is occupied almost continuously with singing. An interesting reaction of the young, especially well developed in this species, is to leave the nest hurriedly and in different directions if disturbed within a few days before the normal time for leaving the nest. The parents often help in this by coaxing and urging the young birds away from the intruder near the nest.

Fox sparrows remain on or near their nesting ground in the far north until near the end of August when they abruptly disappear.

It is evident from the foregoing condensed account of the natural history of the fox sparrow that many phases of its life-history are too little known. Especially desirable is more recorded information concerning the behavior of the birds through the breeding season. It is hoped that this summary of the available literature may serve as a basis for a more thorough investigation of the natural history of *Passerella iliaca*.

## MATERIAL AND ACKNOWLEDGMENTS

It was necessary to go into the field personally, in many selected localities, in order to procure the desired material for this study. Accordingly, specimens were collected and field observations were made by me for use in this particular problem in these localities, all in California unless otherwise stated, and at the time indicated:

1. Berkeley, Alameda County. Specimens were taken in the winter of 1925-26 in the hills near Berkeley.
2. San Geronimo, Marin County. The writer and E. R. Hall collected 39 winter visitant fox sparrows in this vicinity on January 6, 1926.
3. Divide twelve miles north of North Yolla Bolly Mountain, 4,400 feet, Trinity County; May 4 to 21, 1926.
4. Manzanita Lake, 6,000 feet, Shasta County; June 5 to 12, 1926; three and one-half miles northwest of the base of Mount Lassen.
5. Butte Lake, 6,500 feet, Lassen County; June 13 to 20, 1926; twenty miles east and north of Manzanita Lake.
6. Shields Creek, 5,000 feet, Modoc County; June 22 to 24, 1926.
7. Eagle Peak, Warner Mountains, 7,000 feet, Modoc County; June 25 to July 6, 1926; camp located one-half mile west of Mill Creek and two miles north of an east-west line through Eagle Peak.
8. Joseph Creek, 4,800 feet, Modoc County; July 7, 1926.
9. Hume, 5,300 feet, Fresno County; July 13 to 20, 1926.



10. Shaver Ranger Station, 5,300 feet, Fresno County; July 21 to 31, 1926; on slopes near San Joaquin River.

11. Chiatovich Creek, White Mountains, 8,200 feet, Esmeralda County, Nevada; May 9 to 19, 1927.

12. Indian Creek, White Mountains, 8,300 feet, Mono County; May 23 to 26, 1927.

List of *Passerella* skeletons used in this work

|                            |    |                           |     |
|----------------------------|----|---------------------------|-----|
| <i>iliaca</i> .....        | 10 | <i>fulva</i> .....        | 47  |
| <i>altivagans</i> .....    | 0  | <i>megarhynchus</i> ..... | 1   |
| <i>unalaschensis</i> ..... | 9  | <i>brevicauda</i> .....   | 49  |
| <i>insularis</i> .....     | 0  | <i>canescens</i> .....    | 25  |
| <i>sinuosa</i> .....       | 11 | <i>monoensis</i> .....    | 5   |
| <i>annectens</i> .....     | 8  | <i>mariposae</i> .....    | 157 |
| <i>townsendi</i> .....     | 33 | <i>stephensi</i> .....    | 56  |
| <i>fuliginosa</i> .....    | 39 |                           |     |
| <i>schistacea</i> .....    | 15 | Total .....               | 465 |

In addition to the material contained in the Museum of Vertebrate Zoology many specimens were either loaned or donated for my use by several different individuals and institutions. I wish here to express my appreciation for aid of this kind to the following: Mr. Rudyerd Boulton; Mr. Charles D. Bunker, of the University of Kansas Museum of Birds and Mammals; Mr. Ralph Ellis, Jr.; Dr. Francis Harper; Mr. J. Eugene Law; Mr. Joseph Mailliard; Dr. Loye H. Miller; Mr. James Moffitt; Mr. Harry S. Swarth, of the California Academy of Sciences; Dr. Alexander Wetmore, of the United States National Museum; and Mr. Leo K. Wilson. Mr. James Moffitt merits my special thanks for the series of sixty-five skeletons from the vicinity of Lake Tahoe, California, which he collected and donated to the Museum of Vertebrate Zoology for this study.

Under the auspices of the California Museum of Vertebrate Zoology, I was enabled to carry out a part of the necessary field work as outlined in previous paragraphs and to profit by other privileges which aided this study. Much of the success of the field trip to the White Mountains, in 1927, was due to the special interest of Miss Annie M. Alexander in this problem. An award for the year 1927-28, of a Research Assistantship supported in the Museum of Vertebrate Zoology by Miss Alexander, enabled me to give full time, latterly, for the prosecution of this work. The many suggestions and aids received from Dr. Joseph Grinnell throughout the period of this study were valued and appreciated.

Helpful suggestions were received from Mr. Harry S. Swarth, who also identified many of the birds made into skeletons. Mrs. Mary A. Linsdale assisted in the preparation of the skeletons.

## METHODS

### PREPARATION OF SPECIMENS

Although the methods of preparing bird skeletons for study are simple, it becomes necessary to devise and make use of many time-saving contrivances when large numbers of specimens must be made ready within a short time. Collectors of birds, as a rule, are interested in preserving skins only. Because there is little printed information giving directions for the preparation of material such as used in this study, it is thought desirable to record here somewhat in detail the various steps used in the collection and treatment of the material used.

After each day's collecting two labels were made out for each specimen, a temporary label bearing the collector's initial, the field number, and the sex of the specimen, and a permanent label to be kept with the cleaned skeleton. On the permanent label were recorded the name of the subspecies to which the specimen belonged, sex, locality, altitude, date, collector's name, field number, and the weight of the specimen to the nearest .1 gram. All the information on this label was also placed in the field notebook along with more complete data on the habitat and behavior of the living bird.

In order to save time a definite sequence of steps was used in roughing out the skeletons. Long feathers of wings and tail were clipped off with scissors; skin pulled off the body with the fingers and cut with scissors around base of bill; largest muscles of the breast and legs were cut off with scalpel or scissors; eyes and viscera removed with forceps; sex determined; temporary label sewed to the furcula.

The next step was to soak the skeletons in water from twelve to twenty-four hours in order to remove blood clots and to start maceration. This, although not absolutely necessary, saved time in later stages of the cleaning process. The skeletons were removed from water and dried in shade to prevent warping of the bones.

When the time arrived for cleaning the bones in the laboratory the skeletons were wrapped and tied separately in small pieces of cheesecloth. From twenty to thirty were placed in a pan, covered with tap water, and permitted to macerate in a warm place for several days until the flesh loosened. After this the lot was boiled in a dilute ammonia solution (20 cc. to 1 qt. water) in order to soften the ligaments. The remaining pieces of flesh which still clung to the bones

were washed off under a tap or picked off with forceps. After the bones had dried for twelve hours on towel paper they were placed in small glass vials. Next, the skeletons were catalogued as museum specimens and the catalogue numbers were placed, in black ink, on each of the larger bones.

### MEASUREMENT

At first, gross comparisons were made between various elements of the skeletons both within each subspecies and between different subspecies. This gross inspection of the bones also showed what measurements might indicate best the nature of the variation.

All linear measurements were made with a caliper with a large dial on which measurements could be read easily and accurately to one-tenth of a millimeter. In each case only one measurement was taken but care was exercised to make all measurements of one kind as nearly as possible in the same way. In paired elements the same side was always measured unless broken, in which case the other was used.

In selecting characters to be measured, care was taken to make the direction of measurement parallel the direction of growth of the bone or at least, in the case of long bones, to parallel the long axis of the bone. The possibility of warping or other damage was considered in each case and those characters were chosen which appeared to be free from error from this source. Because of the small size of many of the bones of a fox sparrow and the accompanying difficulty of obtaining accurate measurements of these, the number of suitable characters was much smaller than might have been used in a larger species. It is thought, however, that a sufficient number was used to show the chief lines of variation in the internal structure of the species considered.

### DRAWING

Outline drawings of the bones were made with the aid of a camera which was mounted on a vertical stand and so arranged that, when focused on the object directly underneath, the image on the ground glass was twice natural size. The outline was made on tissue paper and was then transferred to drawing paper and the lines traced with india ink. An electric desk lamp was used to reflect sufficient light from the bone. To obtain a clear image on the ground glass, the work was done in a photographic dark-room.

## CHARACTERS USED

*Weight of bird.*—The birds were weighed at the end of each day's collecting. The time between the shooting of the specimen and weighing it varied from a few minutes to several hours. Cenco agate balance scales, accurate to one-tenth of a gram, were used.

*Length of skull.*—The perpendicular distance was measured between two planes; one through the anterior tip of the premaxilla and the other touching the posteriormost point of the skull. The reliability of this measurement is lessened by the presence of the hinge-like joint between the upper jaw and the cranium. In some skulls this joint is so flexible as to prevent accurate measurement. In others, apparently rigid, it is evident that drying has changed this distance from what it would normally be. It was finally decided that this measurement was too misleading to be used so this character was not included in the final tables.

*Width of skull at lacrimal.*—This measurement represented the length of a line connecting the outermost points of the two lacrimal bones. A few skulls were damaged sufficiently to prevent the taking of this measurement. Although the measured distance is a short one, no other measurement on the skull could be devised with so little error from mechanical causes.

*Greatest width of skull.*—The greatest width of skull was measured between the outermost points of the auditory bullae. Except for a few skulls with broken bullae this measurement was easily taken and was reliable.

*Length of ramus* (fig. I, *i*).—This represents the distance from the anterior tip of the mandible to the posteriormost point of the condyle. This measurement parallels the direction of the longest axis of growth of the mandible and, except in those cases where the tip had been damaged in cleaning, was considered to be reliable. Although less desirable because of its shortness, this measurement was thought to be much more reliable than the total length of the skull and it was used in preference to that measurement in making comparisons of variation in size of the head.

*Height of the ramus* (fig. I, *i*).—This represents the perpendicular distance from a plane through the three lowermost points of the mandible to the highest point of one ramus. This measurement proved to be one of the most variable geographically, while at the same time individual variation within a population was not much greater than in other parts of the skeleton.

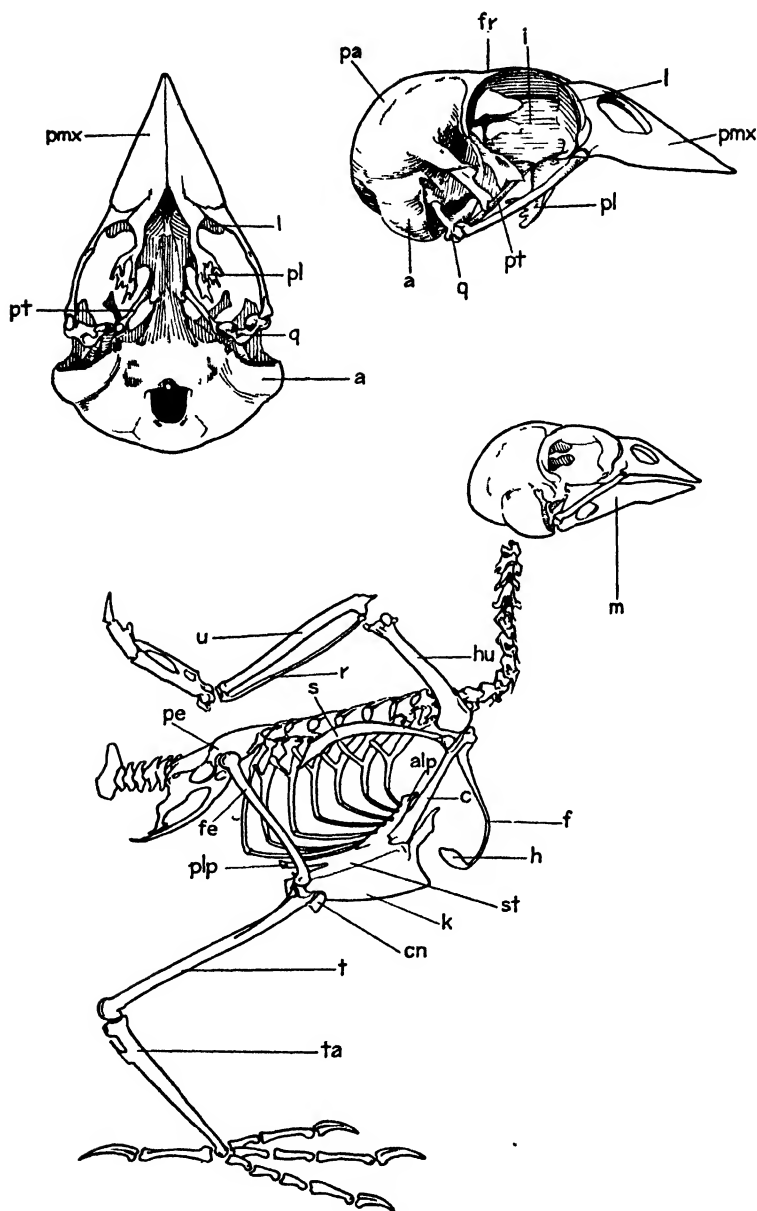


Fig. H. Two views of skull of *Passerella iliaca mariposae*, no. 48791, ♂,  $\times 1\frac{1}{2}$ , and side view of skeleton of *Passerella iliaca canescens*, no. 51153, ♀,  $\times 1$ , labeled to show application of terms used in this paper. Drawn by Frieda Abernathy. Explanation: *l*, lacrimal; *pl*, palatine; *pmx*, premaxilla; *a*, auditory bulla; *h*, hypocleideum; *i*, interorbital septum; *c*, coracoid; *s*, scapula; *f*, furcula; *fe*, femur; *t*, tibia (or tibio-tarsus); *ta*, tarsus (or tarso-metatarsus); *u*, ulna; *r*, radius; *hu*, humerus; *pe*, pelvis; *k*, keel; *st*, sternum; *m*, mandible; *plp*, posterior lateral process; *alp*, anterior lateral process; *cn*, cnemial crest; *fr*, frontal; *pa*, parietal; *q*, quadrate; *pt*, pterygoid.

*Length of sternum* (fig. I, k).—This is the length of a straight line connecting the tip of the manubrium, between the external spines, with the posteriormost point of the body of the sternum. This measurement was subject to little error from damage to the bone.

*Width of sternum* (fig. I, k).—Width of sternum is the shortest distance between the lateral margins of the sternum, taken between anterior and posterior lateral processes. This measurement is less

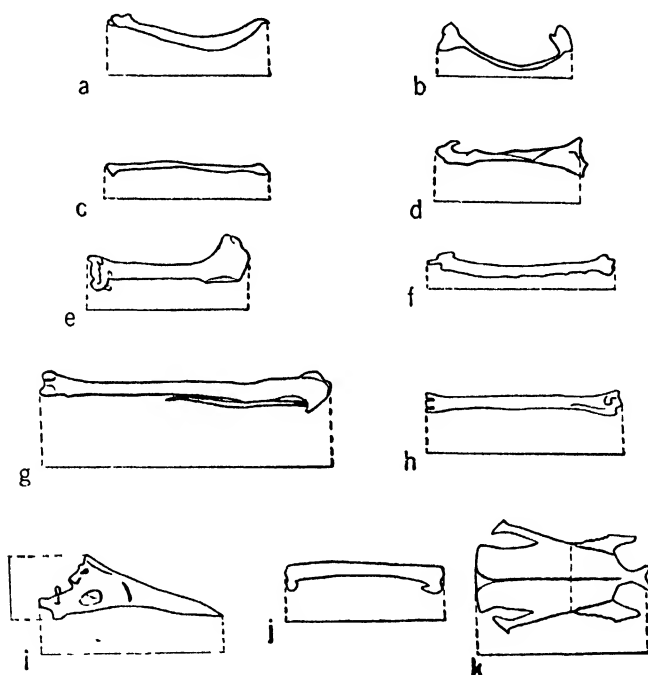


Fig. I. Sketches of bones of *Passerella iliaca* ( $\times 1$ ) showing points between which measurements were taken. *a*, scapula; *b*, furcula; *c*, radius; *d*, coracoid; *e*, humerus; *f*, ulna; *g*, tibio-tarsus (tibia); *h*, tarso-metatarsus (tarsus); *i*, ramus; *j*, femur; *k*, sternum.

reliable than the length of sternum because the bone, being less rigid in this direction, is more subject to warping in drying and also it is easily compressed by the caliper in taking the measurement.

*Length of pelvis*.—The distance was measured from the anterior face of the first fused centrum to the posterior face of the last fused centrum of the pelvis. This measurement varied on account of the difference in number of fused vertebrae which was dependent upon the individual and to some extent upon age. On account of this factor, measurements of length of pelvis could not be depended upon as an accurate index of variation of this character.

*Length of femur* (fig. I, j).—The greatest length from the top of the greater trochanter to the lowest point of the external condyle was measured. This measurement was one of the least subject to error in taking.

*Length of tibia* (fig. I, g).—This measurement was taken from the top of the cnemial ridges to the lower tip of the outer condyle. It was the longest measurement used and consequently was less influenced by instrumental error than in the case of the shorter bones. This was considered to be the most reliable character although it was not the least variable.

*Length of tarsus* (fig. I, h).—Length of tarsus was taken from the top of the intercondylar tubercle to the lower margin of the third trochlea. This character was subject to very little error in measurement.

*Length of humerus* (fig. I, e).—The humerus was measured from the articular head to the tip of the lateral epicondyle. No important sources of error in measurement were discovered.

*Length of radius* (fig. I, c).—The greatest length of this bone was taken parallel to the shaft as shown in the diagram. Care was taken, that too much pressure was not exerted in measuring, to prevent bending of the bone.

*Length of ulna* (fig. I, f).—The distance from the tip of the olecranon to the tip of the carpal head was measured. This bone is sufficiently strong to make possibility of error small.

*Length of coracoid* (fig. I, d).—This bone was measured from the tip of the acrocoracoid to the center of the base. The measurement was thought to be as reliable as any that were taken.

*Length of scapula* (fig. I, a).—The distance measured may be represented by a line from the acromion to the apex of the scapula. This character was one of the less reliable because of the ease with which the apex of the bone might be damaged in preparation. The error in measurement was not large enough, however, to conceal the geographic variability.

*Length of furcula* (fig. I, b).—The diagram shows clearly the manner of taking this measurement which proved to be the least reliable of all those used. The bone being so light and so irregular in shape was easily warped so that a considerable error might be induced in the attempt to measure length. Notwithstanding this difficulty, some use was made of the measurements, although it must be kept in mind that the original values were subject to a considerable amount of error.

## VARIATIONS IN INTERNAL STRUCTURE

## WEIGHT

Variation in body-weight, which can be considered in this analysis, may be conveniently and profitably separated into classes due to age, sex, season, individual, and geography. The influence of each of these factors, as well as that of others less tangible, might be considered as contributing to the wide range of variation in this characteristic.

For studying the influence of age on body-weight only two classes of individuals were used in this work. All weights of birds, determined by the collectors as young, were placed in one age-class. These birds were practically all less than six months old. Table 4 shows that of the twenty-four chances for comparison of young with adult weights, in which race and sex are the same, the average of weights of young birds is larger in nine cases and equal to the average of the adults in a tenth case. Hence, it appears likely that age, in fox sparrows more than one month old, is not important in determining body-weight. Confirmation of this statement is found in the work of Gross (1921, p. 172) to the effect that weights of young dickcissels had nearly reached those of the adults by the eighteenth day after hatching.

The effects of sex and season upon body-weight are so intermingled that it was difficult to separate them sufficiently for a clear interpretation of each. It is thought, however, that the data available are sufficient to establish the truth of the assertions made here.

Although only a little over two-thirds as many weights of females were available as of males, the proportions were about the same in the various race-groups. The average of all the available weights of males (362), irrespective of age, season, or locality, is 32.19 grams. The average weight of all females (239), is 31.52 grams. This average of weights of females is approximately 98 per cent of the average for the males. In each of the three series (*brevicauda*, *mariposae*, and *fulva*) which were collected in the early part of the breeding season, the average of the weights of the females is nearly equal to, or slightly greater than, that of males. In these cases the effect of season, or rather of the reproductive cycle, appears to be such as to offset the difference in weights of the sexes. At the time of egg-laying it seems probable that the females would gain in weight in an amount partly



sufficient to provide the material needed for egg production. Considering this factor, it is probable that during the early breeding season the two sexes in fox sparrows are nearly equal in weight. At

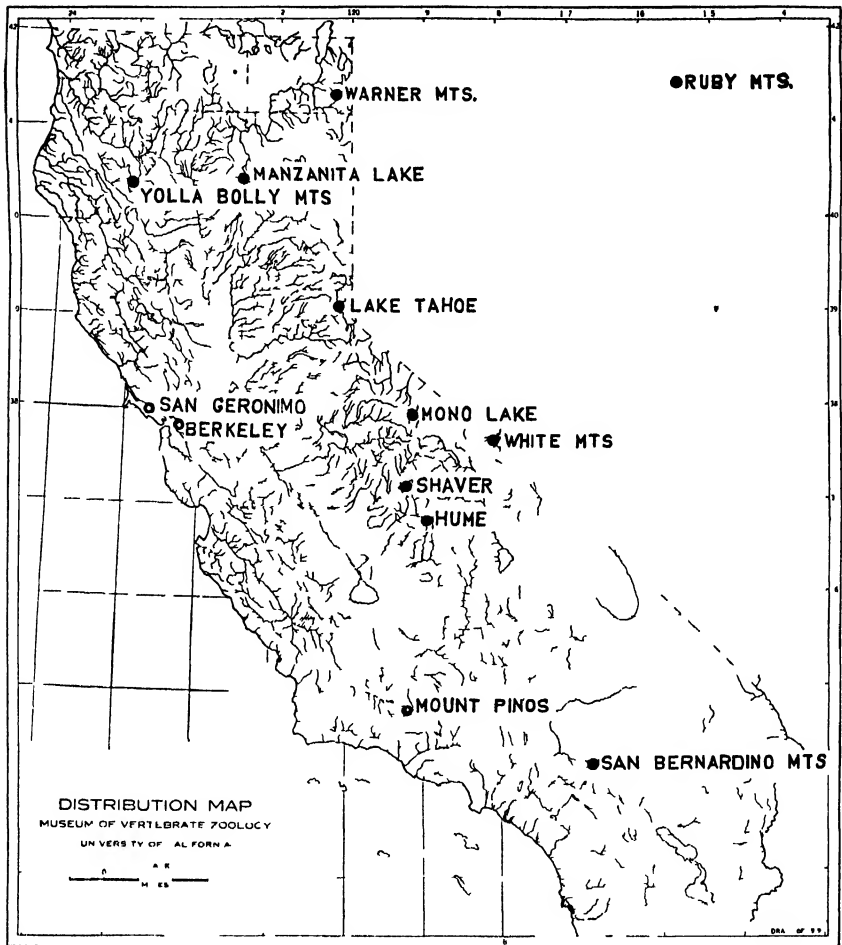


Fig J Map showing principal localities from which skeletons of *Passerella iliaca* were obtained. In the following list are given the names to which birds from each locality were assigned: Warner Mountains, *fulva*; Ruby Mountains, *schistacea*; Manzanita Lake, *mariposae* M; Lake Tahoe, *mariposae* T; Shaver, *mariposae* S; Yolla Bolly Mountains, *brevicauda*; Mono Lake, *monoensis*; White Mountains, *canescens*; Hume, *stephensi*; Mount Pinos and San Bernardino Mountains, *stephensi*; San Geronimo and Berkeley, all birds from these localities were winter collected and several subspecies were represented.

other seasons the females are slightly lighter than the males; in the available series from those seasons the females, on the average, are approximately 95 per cent as heavy as the males.

Independent of the seasonal variation in weight, due to sex influences, there is also a tendency of another sort for birds of this species to vary in weight according to season. The heaviest individual, which

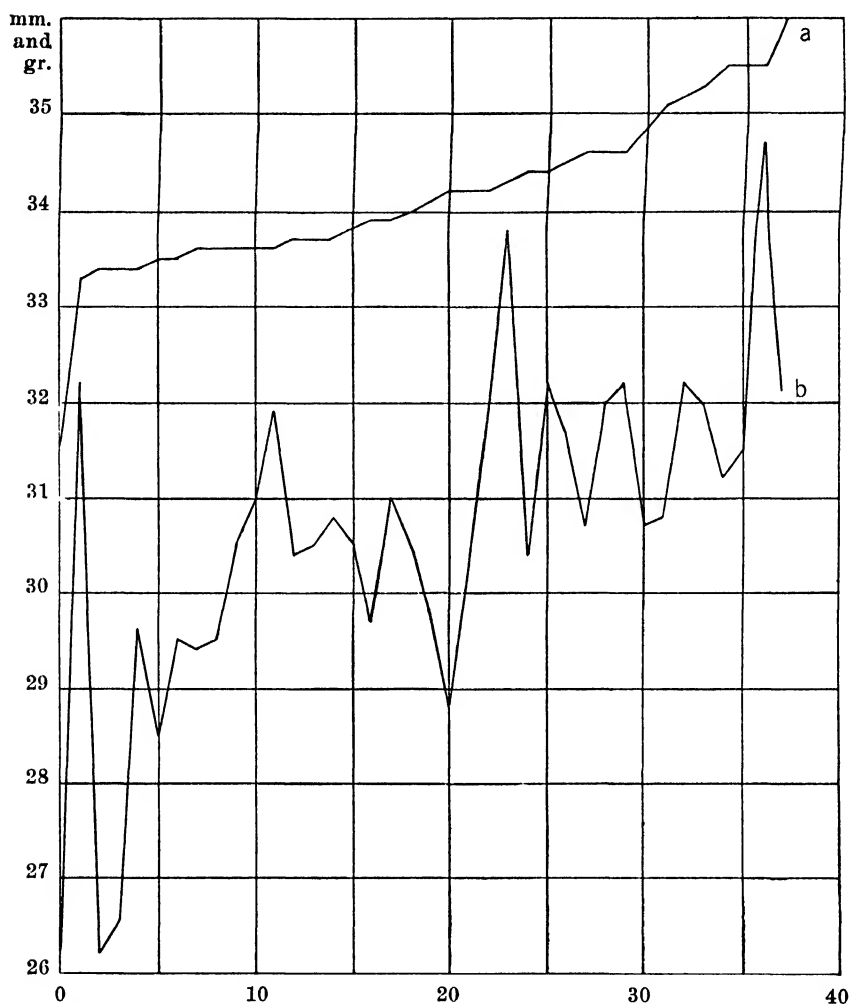


Fig. K. Graph showing variation of weight and length of tibia in a series of thirty-eight males of *mariposae* M. *a*, lengths of tibia when individuals are arranged in order of increasing size; *b*, weights of the same individuals arranged in the same order. Note that if the line *b* were smoothed it would closely parallel line *a*.

weighed fifty grams, was taken in April. Along with other unusually heavy individuals that were taken in March and April, it was noted in the collector's (J. Dixon) field notebook as being especially fat. No doubt there is a tendency at this season, as well as in early fall,

for birds in regions of abundant food supply to store a surplus of energy in the form of fat. In this series, however, with the exception of one or two individuals, evidence of seasonal variation in weight is slight.

Individual variation in weight, as has been pointed out by Howell (1924, p. 988) and others in the case of certain mammals, may be expected to be of a sharper degree than is usually found in linear measurements because three dimensions are involved rather than one.

TABLE 2  
RANGES IN WEIGHT

| Males        | Mean     | Range   | Range<br>Mean   | One-half range<br>Mean |
|--------------|----------|---------|-----------------|------------------------|
|              |          |         | <i>Per cent</i> | <i>Per cent</i>        |
| fulva        | 30 1 gr. | 4 1 gr. | 13 6            | 6 8                    |
| brevicauda   | 34 4     | 8 3     | 24 1            | 12 0                   |
| mariposae M. | 30 7     | 8 3     | 27 0            | 13 5                   |
| mariposae S. | 34 4     | 7 1     | 20 3            | 10 1                   |
| stephensi    | 34 0     | 9 3     | 27 2            | 13 6                   |
| Females      |          |         |                 |                        |
| fulva        | 29 9     | 9 2     | 30 8            | 15 4                   |
| brevicauda   | 34 8     | 10 9    | 31 2            | 15 6                   |
| mariposae M. | 30 5     | 8 9     | 29 2            | 14 6                   |
| mariposae S. | 31 6     | 7 5     | 23 8            | 11 9                   |
| stephensi    | 31 5     | 11 1    | 35 2            | 17 6                   |

In the graph K, *a* represents the individual variation in length of tibia in a series of breeding, adult fox sparrows that were collected at one place and in one season and *b* represents the weights of the same individuals arranged in the same sequence. While there is an evident tendency for the two lines to parallel one another it is also evident that other factors than body size influence individual weights. These factors result in the uneven nature of the line *b*. Among the factors which might contribute to this additional variation are: (1) the amount of undigested food in the stomachs of the individuals, (2) length of elapsed time between shooting of the bird and taking of the weight (this allowing evaporation of the water from the body tissues), (3) general health of the bird, (4) metabolic state of the bird, and (5) instrumental error in weighing (increased when the weights are taken in the field and by different persons). The exact amount of the effect of each of these factors has not yet been determined, but it is thought that they have little effect on the means of large series.

Table 2 has been prepared to show the range in weight in each of five series collected in summer. It shows that in every race the weights of females have a greater range than the weights of males. In *brevicauda* the range for thirty-three males is eight and three-tenths grams; for twenty females it is ten and nine-tenths grams. In the males the range is 24 per cent of the mean; in females, 31 per cent. These facts support the opinion that the females increase in weight during the early part of the nesting season.

A comparison of the coefficients of variation in the various samples (table 3) shows that, although there may be a difference in the degree of variability in weight in the sexes or in the different races of fox

TABLE 3  
VARIABILITY IN WEIGHT

|                          | <i>brevicauda</i> ♀ | <i>brevicauda</i> ♂ | <i>mariposae</i> ♂ | <i>canescens</i> ♂ | <i>Peromyscus</i> | Man            |
|--------------------------|---------------------|---------------------|--------------------|--------------------|-------------------|----------------|
| Number                   | 18                  | 30                  | 38                 | 16                 | 74                | 272            |
| Mean                     | 34 35±0 45 gr       | 34 29±0 26 gr       | 30 67±0 18 gr      | 23 48±0 26 gr      | 12 66±0 10 gr     | 51 56±0 58 lbs |
| Standard deviation       | 2 89±0 32           | 3 13±0 19           | 1 72±0 13          | 1 57±0 19          | 1 28              | 19 95±0 53     |
| Coefficient of variation | 8 41±0 95%          | 6 21±0 54%          | 5 60±0 45%         | 5 33±0 64%         | 10 11%            | 13 16±0 39%    |

sparrows, the data used here do not assure the truth of such a conclusion. Many more weights are needed before the answer to this question can be determined. It appears, however, that variation in weight is less in *Passerella* than in the two mammals where comparisons may be made. Variation in weight in *Passerella*, according to my determination, is slightly more than half that in *Peromyscus*, according to Sumner's results (1926, p. 166), and about one-third that in man according to Pearl (1927, p. 238). When the coefficient of variability of weight in a race of fox sparrows is compared with that for some linear measurement of the skeleton, for example, length of tibia, it becomes evident again that weight is more variable than the size of the bones of the skeleton.

In order to interpret geographic variation in weight it was necessary in this case to first determine whether or not the differences in means of the various samples represented actual differences in the populations or whether they might be due to random sampling. For this purpose a series of weights of males of the subspecies *brevicauda* and a series of weights of males of the subspecies *mariposae* were compared. The difference between the means proved, in this instance,

TABLE 4

## WEIGHTS (IN GRAMS) OF FOX SPARROWS

| Race                      | Males |       |      |      |         |       |      |      |       |       |      |      | Females |       |      |      |         |       |      |      |       |       |      |      | Both sexes, Total |       |      |      |
|---------------------------|-------|-------|------|------|---------|-------|------|------|-------|-------|------|------|---------|-------|------|------|---------|-------|------|------|-------|-------|------|------|-------------------|-------|------|------|
|                           | Adult |       |      |      | Juvenal |       |      |      | Total |       |      |      | Adult   |       |      |      | Juvenal |       |      |      | Total |       |      |      |                   |       |      |      |
|                           | no    | av    | min  | max  | no      | av    | min  | max  | no    | av    | min  | max  | no      | av    | min  | max  | no      | av    | min  | max  | no    | av    | min  | max  | no                | av    | min  | max  |
| <i>altivagans</i>         | 7     | 30.88 | 26.0 | 41.0 | 2       | 30.40 | 29.8 | 31.0 | 9     | 30.77 | 26.0 | 41.0 | 7       | 27.85 | 24.5 | 32.0 | 3       | 28.13 | 25.5 | 29.8 | 10    | 27.94 | 24.5 | 32.0 | 19                | 29.25 | 24.5 | 41.0 |
| <i>unalaschensis</i>      | 1     | 37.80 | 37.8 | 37.8 | 3       | 37.80 | 34.1 | 42.5 | 4     | 37.80 | 34.1 | 42.5 | 4       | 37.42 | 31.3 | 50.0 | 4       | 33.33 | 31.0 | 37.0 | 8     | 35.37 | 31.0 | 50.0 | 12                | 36.18 | 31.0 | 50.0 |
| <i>insularis</i>          | 3     | 38.00 | 35.1 | 41.3 | 1       | 33.70 |      |      | 4     | 36.92 | 33.7 | 41.3 |         |       |      |      | 1       | 34.40 |      |      | 1     |       |      |      | 5                 | 36.42 | 33.7 | 41.3 |
| <i>sinuosa</i>            | 26    | 32.45 | 26.5 | 37.2 | 10      | 33.02 | 27.3 | 37.6 | 36    | 32.61 | 26.5 | 37.6 | 18      | 31.73 | 25.8 | 37.2 | 10      | 33.36 | 30.5 | 36.9 | 28    | 32.31 | 25.8 | 37.2 | 64                | 32.48 | 25.8 | 37.6 |
| <i>annectens</i>          | 5     | 36.48 | 32.5 | 41.8 | 2       | 36.75 | 35.3 | 38.2 | 7     | 36.55 | 32.5 | 41.8 | 5       | 33.72 | 31.0 | 36.7 | 8       | 33.97 | 31.5 | 38.2 | 13    | 33.87 | 31.0 | 38.2 | 20                | 34.81 | 31.0 | 41.8 |
| <i>fuliginosa</i>         | 3     | 35.56 | 34.4 | 36.2 | 11      | 35.44 | 32.6 | 39.5 | 14    | 35.47 | 32.6 | 39.5 | 5       | 33.42 | 31.0 | 34.0 | 5       | 32.14 | 28.7 | 34.1 | 10    | 32.78 | 28.7 | 34.1 | 24                | 34.35 | 28.7 | 39.5 |
| <i>schistacea</i>         | 14    | 28.92 | 25.5 | 32.4 | 9       | 27.87 | 23.3 | 34.1 | 23    | 28.51 | 23.3 | 34.1 | 8       | 26.50 | 23.5 | 29.7 | 3       | 25.70 | 25.0 | 26.8 | 11    | 26.28 | 23.5 | 29.7 | 34                | 27.79 | 23.3 | 34.1 |
| <i>fulva</i>              | 19    | 30.14 | 28.0 | 32.1 | 8       | 28.51 |      |      | 27    | 29.66 | 26.5 | 32.1 |         |       |      |      |         |       |      | 16   | 29.92 | 25.7  | 35.5 | 43   | 29.75             | 25.7  | 35.5 |      |
| <i>megarrhynchus</i>      | 2     | 28.00 | 26.0 | 30.0 |         |       |      |      | 2     |       |      |      |         |       |      |      | 1       | 32.50 |      |      |       |       |      |      | 3                 | 29.50 | 26.0 | 32.5 |
| <i>brevicauda</i>         | 33    | 34.37 | 30.3 | 38.6 |         |       |      |      | 33    |       |      |      | 20      | 34.78 | 30.5 | 41.4 |         |       |      | 20   |       |       |      | 53   | 34.44             | 30.3  | 41.4 |      |
| <i>canescens</i> (summer) | 16    | 29.48 | 26.5 | 32.7 |         |       |      |      | 16    | 29.48 | 26.5 | 32.7 | 7       | 29.17 | 24.8 | 35.3 |         |       |      | 7    | 29.17 | 24.8  | 35.3 | 23   | 28.95             | 24.8  | 35.3 |      |
| <i>canescens</i> (MVZ)    | 9     | 30.05 | 27.3 | 32.7 | 2       | 26.45 | 25.6 | 27.3 | 11    | 29.40 | 25.6 | 32.7 | 3       | 28.36 | 26.3 | 30.3 | 6       | 28.41 | 26.0 | 30.6 | 9     | 28.40 | 26.0 | 30.6 | 20                | 28.95 | 25.6 | 32.7 |
| <i>monacensis</i>         | 31    | 31.27 | 27.0 | 36.6 | 3       | 29.60 | 29.3 | 30.0 | 34    | 31.12 | 27.0 | 36.6 | 17      | 30.56 | 27.8 | 36.0 | 1       | 32.50 |      | 18   | 30.84 | 27.8  | 36.0 | 52   | 30.96             | 27.0  | 36.6 |      |
| <i>mariposae</i> M        | 38    | 30.67 | 26.5 | 34.8 |         |       |      |      | 38    |       |      |      | 15      | 30.53 | 26.2 | 35.1 |         |       |      | 15   |       |       |      | 53   | 30.63             | 26.2  | 35.1 |      |
| <i>mariposae</i> S        | 23    | 34.44 | 30.6 | 37.7 | 4       | 28.75 |      |      | 27    | 33.60 | 25.7 | 37.7 |         |       |      |      |         |       |      | 25   | 31.56 | 28.2  | 35.7 | 52   | 32.62             | 25.7  | 37.7 |      |
| <i>mariposae</i> (MVZ)    | 22    | 30.74 | 26.3 | 34.0 | 2       | 31.85 | 31.0 | 32.7 | 24    | 30.83 | 26.3 | 34.0 | 18      | 31.70 | 26.3 | 41.5 | 3       | 28.93 | 26.9 | 31.8 | 21    | 31.31 | 26.3 | 41.5 | 45                | 31.05 | 26.3 | 41.5 |
| <i>stephens</i> (Hume)    | 21    | 34.01 | 29.3 | 38.6 | 10      | 32.25 | 28.1 | 36.1 | 31    | 33.44 | 28.1 | 38.6 |         |       |      |      |         |       |      | 18   | 31.53 | 25.2  | 36.3 | 49   | 33.40             | 25.2  | 38.6 |      |
| <i>stephens</i> (MVZ)     | 7     | 36.11 | 33.5 | 40.0 | 15      | 36.50 | 28.5 | 41.2 | 22    | 36.37 | 28.5 | 41.2 | 6       | 35.50 | 31.0 | 40.9 | 2       | 35.20 | 32.3 | 38.1 | 8     | 36.17 | 31.0 | 40.9 | 30                | 36.12 | 28.5 | 41.2 |
| Summary                   | 280   |       | 25.5 | 41.8 | 82      |       | 23.3 | 42.5 | 362   | 32.19 | 23.3 | 42.5 | 133     |       | 23.5 | 50.0 | 47      |       | 25.0 | 38.1 | 239   | 31.52 | 23.5 | 50.0 | 601               | 31.92 | 23.3 | 50.0 |

to be unquestionably due to a difference in the populations from which the samples were taken.

Next the means of the various samples may be compared with one another and their arrangement compared with the distribution of samples as indicated on the map (fig. J). It is easily seen that the average body-weight of these samples is a useful characteristic, to be used along with others for making racial distinctions.

To summarize: age in fox sparrows more than one month old is apparently of little importance in influencing weight.

Males in this species, on the average, weigh slightly more than females.

There is a tendency for birds in this species to increase in weight in spring and fall.

Individual variation is greater in weight than in linear measurements of bones.

Geographic variation in weight parallels that of some other characteristics, especially those that have been used in systematic studies of this species.

#### SKELETON

*Width of skull at lacrimal and greatest width of skull.*—In the systematic study of mammals the skull has been considered, for a long time, an essential part of the materials to be used along with the skin of the animal. Ornithologists, unfortunately, have never used the skulls of birds in their systematic work, possibly, because of the impracticability of saving for study both the skin and the skull of the same individual. Aside from this difficulty, which is really a serious one, it must be recalled that birds are without teeth which are of great value in mammalian studies, and that as a rule the bird's skull is more fused than is generally the case in mammals. The series of skulls of *Passerella iliaca* used in this work, however, varies as much as, if not more than, a comparable series of skulls of any species of the smaller North American mammals varies.

Variation in these, as in other characters considered, may be due to several causes each of which must be considered separately in an attempt to analyze variability in the species. The first of these major causes to be considered is age. In very young birds the separate bones of the skull may be distinguished but this transitory condition is soon replaced by that found in the adult. A specimen of *P. i. fulva* (no. 48856, Calif. Mus. Vert. Zool.) was taken just after it had left the nest and before its feathers had fully developed. In this specimen

practically all the sutures in the skull have closed but the lines of fusion can be easily made out. The bones are all thin and apparently the deposition of calcium is far from complete. Other specimens of young birds, taken at the same time and place and which were only a few days older than this one, had most of their sutures fused so that they could be made out with difficulty.

It is well known to field collectors that young passerine birds may be distinguished from adults by noting the condition of the frontal and parietal bones in the young. Young have only one layer of bone in this region of the cranium, while adults have two layers with connecting rods, which appear as dots when viewed by the aid of transmitted light. The area of single layered bone becomes smaller and smaller until it entirely disappears, in the case of *Passerella*, at a little over six months of age.

In the skulls of mammals, age is considered to be indicated by the stage of development of ridges and other places of attachment for muscles. In one or two series of skulls of *P. iliaca* two groups were selected, one of which showed better developed ridges than the other. In each instance the group with better developed ridges averaged slightly larger than the other group but the difference was so small that no further attempt was made to establish age groups by this method. The very young birds' skulls were markedly more smooth and more rounded than those of older birds. The young birds' skulls were correspondingly smaller than those of older individuals. By the time for the fall migration, however, the differences in size dependent upon age are so small that, in computing averages, separate age groups were not established for birds taken later than that.

As may be seen by reference to the accompanying tables of means, in the case of practically every character and in nearly every group that was measured the females were slightly smaller than the males. The only exceptions to this condition are in samples which were too small for the means to be reliable or in characters in which there might be error in measurement. In plates 16 and 17 are shown upper and lower views of the skulls of eight males and eight females of *brevicauda* that were taken at one location and in the early breeding season. A close inspection of these photographs will show that a slight difference in the sexes may be made out by the eye.

In any one series of skulls of the same sex from a single locality a considerable degree of variability is apparent in the number, size, and arrangement of the openings in the interorbital septum. There are

TABLE 5  
VARIABILITY IN WIDTH OF SKULL AT LACRIMAL  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean      | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|-----------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 4                   | 9.00      | 9.3     | 8.8     | 5     |                    |                                     |
| iliaca       | ♀   | 2                   | 8.75      | 8.9     | 8.6     | 3     |                    |                                     |
| townsendi    | ♂   | 9                   | 8.76      | 9.4     | 8.1     | 1.3   |                    |                                     |
| townsendi    | ♀   | 22                  | 8.55      | 9.4     | 7.8     | 1.6   |                    |                                     |
| fuliginosa   | ♂   | 16                  | 8.63      | 9.2     | 7.8     | 1.4   |                    |                                     |
| fuliginosa   | ♀   | 19                  | 8.36      | 9.0     | 7.7     | 1.3   |                    |                                     |
| fulva        | ♂   | 15                  | 8.91      | 9.9     | 8.3     | 1.6   |                    |                                     |
| fulva        | ♀   | 7                   | 8.45      | 9.1     | 8.0     | 1.1   |                    |                                     |
| brevicauda   | ♂   | 26                  | 9.87±0.05 | 10.5    | 9.1     | 1.4   | 38±0.04            | 3.87±0.36                           |
| brevicauda   | ♀   | 11                  | 9.43      | 10.0    | 8.9     | 1.1   |                    |                                     |
| canescens    | ♂   | 15                  | 8.80±0.08 | 9.5     | 8.1     | 1.4   | 44±0.05            | 4.97±0.61                           |
| canescens    | ♀   | 7                   | 8.18      | 9.2     | 7.5     | 1.7   |                    |                                     |
| mariposae M. | ♂   | 30                  | 9.09      | 9.9     | 8.3     | 1.6   |                    |                                     |
| mariposae M. | ♀   | 11                  | 8.82      | 9.4     | 8.1     | 1.3   |                    |                                     |
| mariposae T. | ♂   | 34                  | 9.12±0.03 | 9.7     | 8.6     | 1.1   | 27±0.02            | 2.96±0.24                           |
| mariposae T. | ♀   | 14                  | 8.83±0.07 | 9.7     | 8.4     | 1.3   | 38±0.05            | 4.25±0.54                           |
| mariposae S. | ♂   | 21                  | 9.74      | 10.5    | 8.6     | 1.9   |                    |                                     |
| mariposae S. | ♀   | 15                  | 9.25      | 9.9     | 8.7     | 1.2   |                    |                                     |
| stephensi    | ♂   | 16                  | 9.88      | 10.9    | 9.1     | 1.8   |                    |                                     |
| stephensi    | ♀   | 10                  | 9.44      | 10.5    | 8.8     | 1.7   |                    |                                     |

NOTE. M = Manzanita Lake, T = Lake Tahoe, S = Shaver



also some individual differences in the number and arrangement of the prongs or divisions of the palatine bones. Some of the rugosity mentioned in the account of age variation is likely due to an individual variation. The series of skulls shown on plates 16 and 17 were random

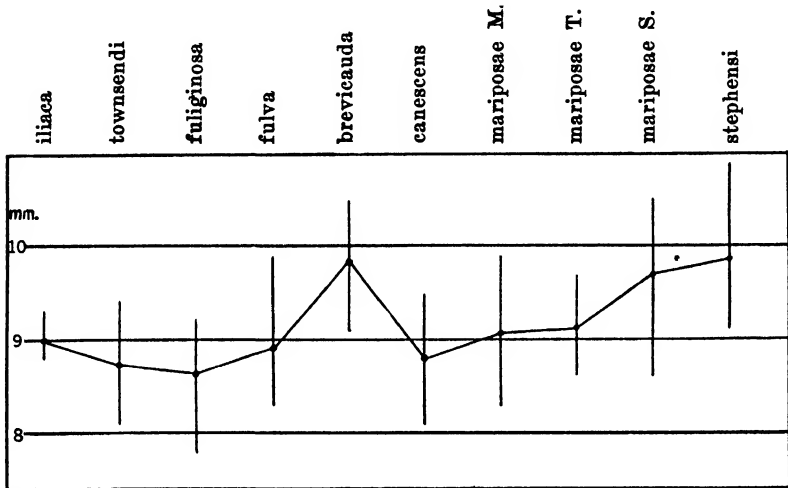


Fig. L. Diagram showing individual and geographic variation in width of skull at lacrimal for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

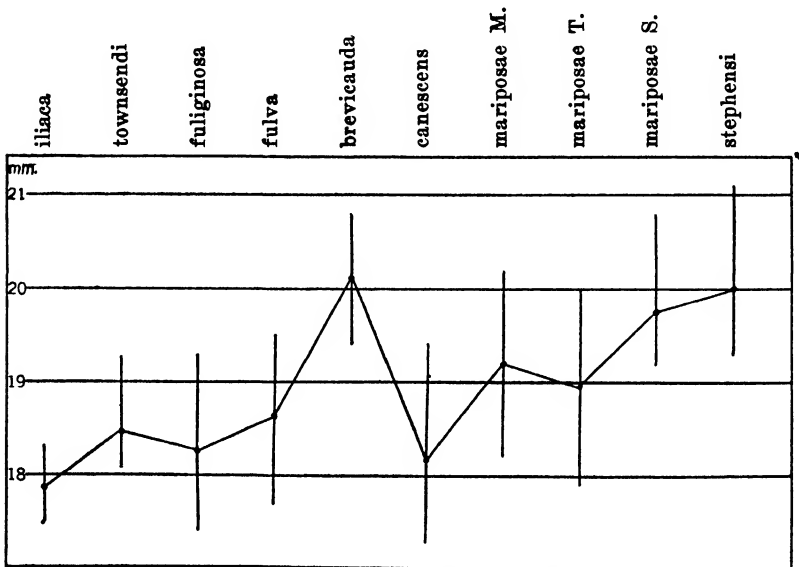


Fig. M. Diagram showing individual and geographic variation in greatest width of skull for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

TABLE 6  
VARIABILITY IN GREATEST WIDTH OF SKULL  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 4                   | 17 85      | 18 3    | 17 5    | 8     |                    |                                     |
| iliaca       | ♀   | 3                   | 17 83      | 18 1    | 17 7    | 4     |                    |                                     |
| townsendi    | ♂   | 5                   | 18 48      | 19 3    | 18 1    | 1 2   |                    |                                     |
| townsendi    | ♀   | 18                  | 18 08±0 16 | 18 5    | 17 5    | 1 0   | 1 00±0 11          | 5 51±0 62                           |
| fuliginosa   | ♂   | 13                  | 18 28      | 19 3    | 17 4    | 1 9   |                    |                                     |
| fuliginosa   | ♀   | 18                  | 17 83±0 06 | 18 4    | 17 1    | 1 3   | 36±0 04            | 2 04±0 23                           |
| fulva        | ♂   | 15                  | 18 62      | 19 5    | 17 7    | 1 8   |                    |                                     |
| fulva        | ♀   | 8                   | 18 21      | 18 6    | 17 7    | 9     |                    |                                     |
| brevicauda   | ♂   | 25                  | 20 12±0 04 | 20 8    | 19 4    | 1 4   | 32±0 03            | 1 59±0 15                           |
| brevicauda   | ♀   | 13                  | 19 63      | 20 2    | 18 7    | 1 5   |                    |                                     |
| canescens    | ♂   | 13                  | 18 19±0 10 | 19 4    | 17 3    | 2 1   | 56±0 07            | 3 08±0 41                           |
| canescens    | ♀   | 6                   | 17 51      | 18 5    | 16 1    | 2 4   |                    |                                     |
| mariposae M. | ♂   | 30                  | 19 21      | 20 2    | 18 2    | 2 0   |                    |                                     |
| mariposae M. | ♀   | 14                  | 18 68      | 19 3    | 17 9    | 1 4   |                    |                                     |
| mariposae T. | ♂   | 23                  | 18 95±0 07 | 20 0    | 17 9    | 2 1   | 48±0 05            | 2 55±0 25                           |
| mariposae T. | ♀   | 10                  | 18 84±0 09 | 19 5    | 18 2    | 1 3   | 43±0 06            | 2 28±0 34                           |
| mariposae S. | ♂   | 21                  | 19 78      | 20 8    | 19 2    | 1 6   |                    |                                     |
| mariposae S. | ♀   | 14                  | 19 28      | 20 0    | 18 6    | 1 4   |                    |                                     |
| stephensi    | ♂   | 13                  | 20 00      | 21 1    | 19 3    | 2 8   |                    |                                     |
| stephensi    | ♀   | 10                  | 19 61      | 20 6    | 19 0    | 1 6   |                    |                                     |

selections photographed to show the normal individual variation encountered in a group of this species from one locality.

The greatest range in total width of the skull was (2.8 mm.) that in a series of thirteen *stephensi* males from Hume. The greatest range in the width of the skull at the lacrimal was (1.9 mm.) found in a series of twenty-one male *mariposae* from Shaver.

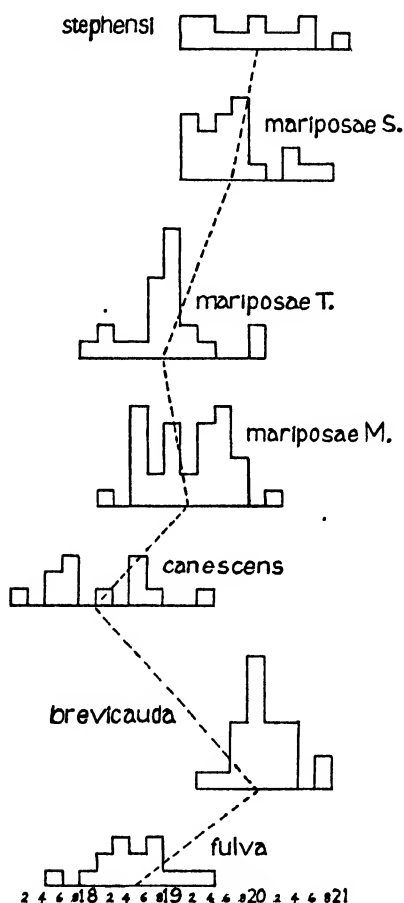


Fig. N. Histograms showing frequency distributions of values for greatest width of skull in seven samples of males.

Standard deviations and variability coefficients have been computed for a few races but the numbers of individuals are too small in most instances for these values to be thoroughly reliable. It is evident, however, that individual variation in size in these characters is not great in this species.

TABLE 7  
VARIABILITY IN LENGTH OF RAMUS  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 4                   | 22 65      | 22 8    | 22 3    | 5     |                    |                                     |
| iliaca       | ♀   | 2                   | 21 90      | 22 3    | 21 5    | 8     |                    |                                     |
| townsendi    | ♂   | 8                   | 23 03      | 23 9    | 21 6    | 2 3   |                    |                                     |
| townsendi    | ♀   | 20                  | 22 53±0 08 | 23 3    | 21 5    | 1 8   | 54±0 06            | 2 41±0 26                           |
| fuliginosa   | ♂   | 11                  | 22 84      | 23 6    | 21 4    | 2 2   |                    |                                     |
| fuliginosa   | ♀   | 16                  | 22 30±0 09 | 23 0    | 21 0    | 2 0   |                    |                                     |
| fulva        | ♂   | 15                  | 22 44      | 23 3    | 20 6    | 2 7   | 55±0 07            | 2 48±0 30                           |
| fulva        | ♀   | 5                   | 21 80      | 22 8    | 21 0    | 1 8   |                    |                                     |
| brevicauda   | ♂   | 28                  | 24 56±0 07 | 25 7    | 23 3    | 2 4   | 57±0 05            | 2 30±0 21                           |
| brevicauda   | ♀   | 16                  | 24 43±0 08 | 25 2    | 23 3    | 1 9   | 51±0 06            |                                     |
| canescens    | ♂   | 14                  | 21 98±0 12 | 23 5    | 20 9    | 2 6   | 67±0 08            | 3 03±0 39                           |
| canescens    | ♀   | 6                   | 21 11      | 21 9    | 20 6    | 1 3   |                    |                                     |
| mariposae M. | ♂   | 34                  | 22 98±0 06 | 24 4    | 21 8    | 2 6   | 57±0 07            | 2 50±0 20                           |
| mariposae M. | ♀   | 14                  | 22 74±0 10 | 23 9    | 21 8    | 2 1   | 54±0 07            | 2 41±0 31                           |
| mariposae T. | ♂   | 30                  | 22 90±0 09 | 24 3    | 21 6    | 2 7   | 73±0 06            | 3 19±0 28                           |
| mariposae T. | ♀   | 17                  | 22 54±0 09 | 23 8    | 21 7    | 2 1   | 56±0 07            | 3 50±0 29                           |
| mariposae S. | ♂   | 17                  | 24 31±0 08 | 25 5    | 23 7    | 1 8   | 52±0 06            | 2 13±0 25                           |
| mariposae S. | ♀   | 16                  | 23 98      | 25 6    | 22 7    | 2 9   | 75                 | 3 14                                |
| stephensi    | ♂   | 24                  | 24 83±0 09 | 26 1    | 23 6    | 2 5   | 65±0 06            | 2 60±0 25                           |
| stephensi    | ♀   | 11                  | 24 62      | 25 2    | 23 7    | 2 5   |                    |                                     |

Of the major classes of variation there remains to be considered, for these characters, that due to geography. Even a cursory examination of the accompanying charts, tables, and photographs will show that differences in the skulls of *Passerella* that can be correlated with geography are greater than those of any class of variability previously considered.

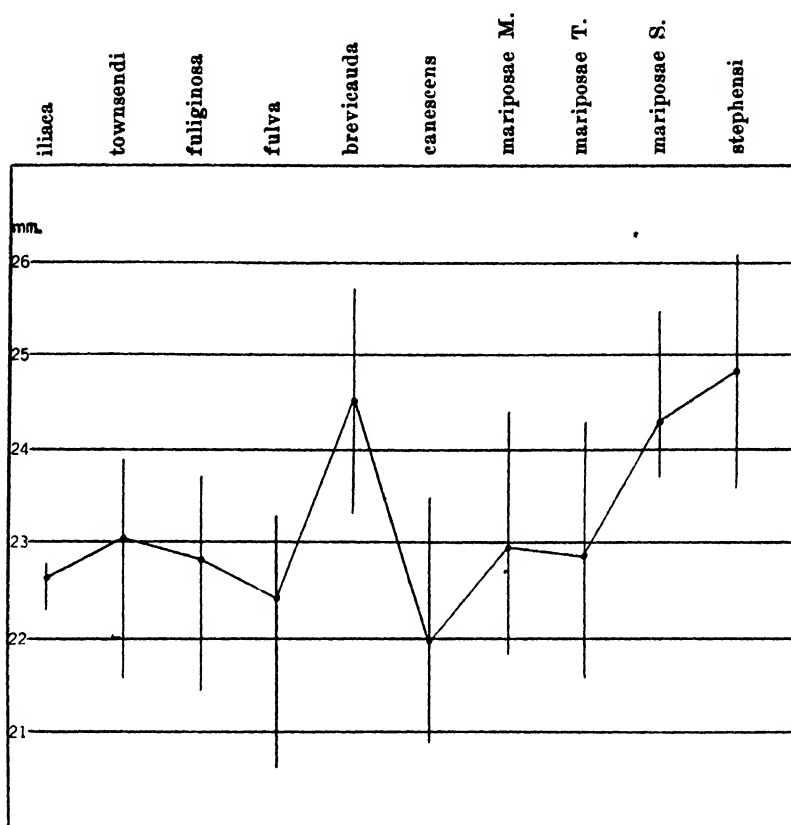


Fig. O. Diagram showing individual and geographic variation in length of ramus for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

The smallest mean value of width of skull at lacrimal for any sample is that of seven female *canescens* (8.18 mm.). The series of smallest males is that of *fuliginosa* whose mean value is 8.63 mm. The group with largest measurements for this character is the series of *stephensi* from Hume. The means of each of the two sexes are respectively .1 mm. larger than those of the next population in size (*brevicauda*).

In the greatest width of skull the series of smallest males is that of *iliaca* (17.85 mm.); females, *canescens* (17.51 mm.). In this character *brevicauda* measures largest in mean values for both sexes although the largest individuals of both sexes are *stephensi*.

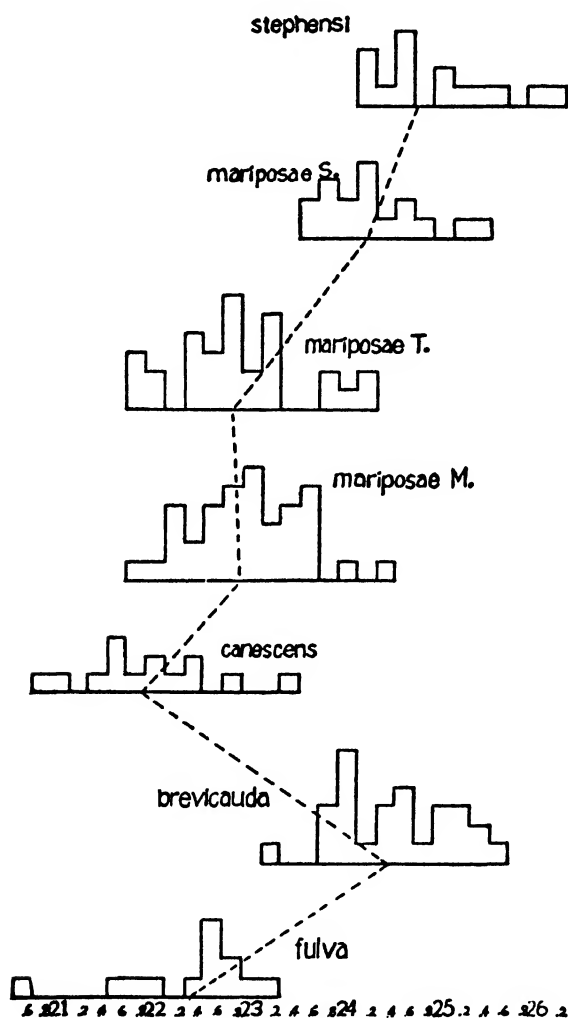


Fig. P. Histograms showing frequency distributions of values for length of ramus in seven samples of males.

When ratios are computed between these two characters it is readily apparent that in the largest skulls (*stephensi*) the width of the skull at lacrimal is greater in proportion to the greatest width of skull than in the case of the smaller skulls (*townsendi* and *fuliginosa*).

TABLE 8

VARIABILITY IN HEIGHT OF RAMUS  
Measurements in millimeters

| Sample              | Sex | Number of specimens | Mean      | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|---------------------|-----|---------------------|-----------|---------|---------|-------|--------------------|-------------------------------------|
| <i>iliaca</i>       | ♂   | 4                   | 6.17      | 6.7     | 5.9     | 8     |                    |                                     |
| <i>ilhaca</i>       | ♀   | 1                   | 5.80      | 5.8     | 5.8     | 0     |                    |                                     |
| <i>townsendi</i>    | ♂   | 8                   | 6.07      | 6.5     | 5.3     | 1.2   |                    |                                     |
| <i>fuliginosa</i>   | ♀   | 20                  | 5.88      | 6.7     | 5.4     | 1.3   |                    |                                     |
| <i>fuliginosa</i>   | ♂   | 12                  | 5.92      | 6.7     | 5.5     | 1.2   |                    |                                     |
| <i>fuliginosa</i>   | ♀   | 18                  | 5.72      | 6.2     | 5.3     | 9     |                    |                                     |
| <i>fulva</i>        | ♂   | 13                  | 7.65      | 8.0     | 7.3     | 7     |                    |                                     |
| <i>fulva</i>        | ♀   | 5                   | 7.24      | 7.6     | 6.9     | 7     |                    |                                     |
| <i>brevicauda</i>   | ♂   | 30                  | 9.64      | 10.6    | 8.9     | 1.7   |                    |                                     |
| <i>brevicauda</i>   | ♀   | 18                  | 9.24      | 10.4    | 8.5     | 1.9   |                    |                                     |
| <i>canescens</i>    | ♂   | 15                  | 6.86±0.11 | 8.2     | 6.3     | 1.9   | 62±0.08            | 9.10±1.12                           |
| <i>canescens</i>    | ♀   | 6                   | 6.33      | 7.0     | 6.0     | 1.0   |                    |                                     |
| <i>mariposae</i> M. | ♂   | 34                  | 8.17      | 8.9     | 7.5     | 1.4   |                    |                                     |
| <i>mariposae</i> M. | ♀   | 14                  | 8.09      | 8.7     | 7.2     | 1.5   |                    |                                     |
| <i>mariposae</i> T. | ♂   | 33                  | 8.33±0.05 | 9.3     | 7.3     | 2.0   | 40±0.03            | 4.78±0.40                           |
| <i>mariposae</i> T. | ♀   | 17                  | 8.01±0.11 | 8.9     | 5.9     | 3.0   | 70±0.08            | 8.73±1.01                           |
| <i>mariposae</i> S. | ♂   | 23                  | 9.13      | 10.1    | 8.2     | 1.9   |                    |                                     |
| <i>mariposae</i> S. | ♀   | 15                  | 8.65      | 9.3     | 7.9     | 1.4   |                    |                                     |
| <i>stephensi</i>    | ♂   | 21                  | 9.42      | 10.6    | 8.6     | 2.0   |                    |                                     |
| <i>stephensi</i>    | ♀   | 11                  | 9.39      | 10.2    | 8.6     | 1.6   |                    |                                     |

*Length and height of ramus* behave, in respect to age and sex variation, in much the same way as the two characters just considered. Individual variation in length of ramus appears to be nearly as extensive as in the first two characters considered. Height of ramus, however, is apparently the most variable individually of all the characters measured. The range in the various groups, while actually not much

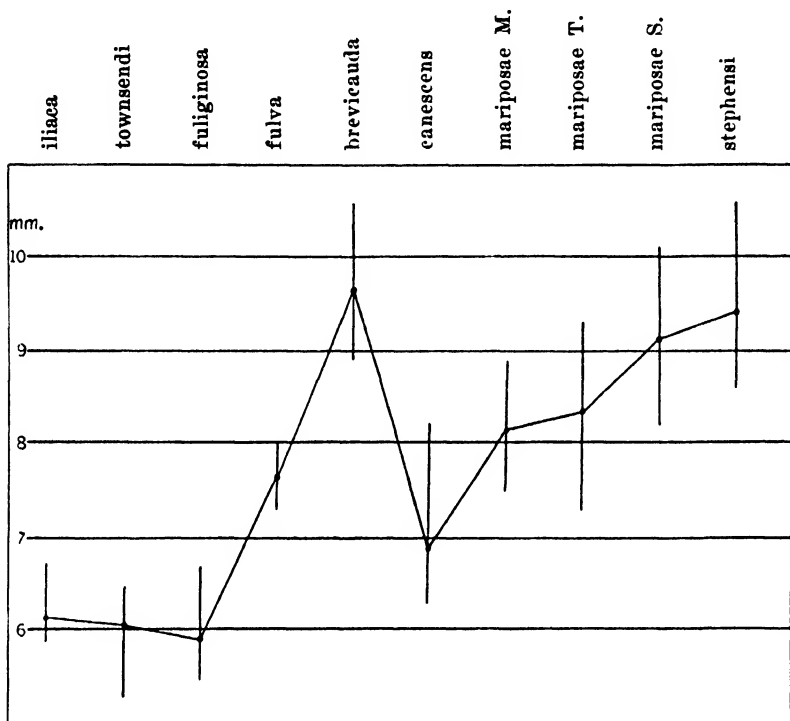


Fig. Q. Diagram showing individual and geographic variation in height of ramus for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

greater for this than for the other characters, is relatively greater because the measurement is so short. The greatest range for any group (*mariposae* T., females) is 37 per cent of the mean value for that group. The greatest range for width of skull at lacrimal (*mariposae* S., males) is less than 20 per cent of the mean value for that group. The variability coefficients for this character, in spite of the small numbers of individuals, are consistently much higher than for any other character.

The mean values for length of ramus are arranged in much the same way as the corresponding values for greatest width of cranium.



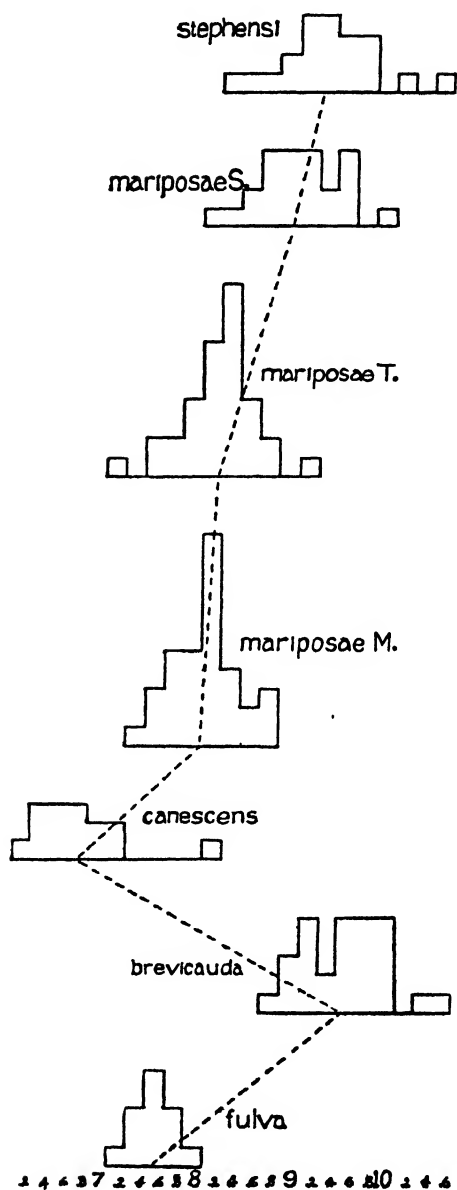


Fig. R. Histograms showing frequency distributions of values for height of ramus in seven samples of males.

Individual measurements of length of ramus range between 20.60 mm. (females of *canescens* and *fulva*) and 26.10 mm. (male *stephensi*). When figures O and Q are compared it is evident that there is not a close correlation between length of ramus and its height. This may be shown by comparing ratios of the mean values of these characters. The following figures represent values obtained by dividing the mean

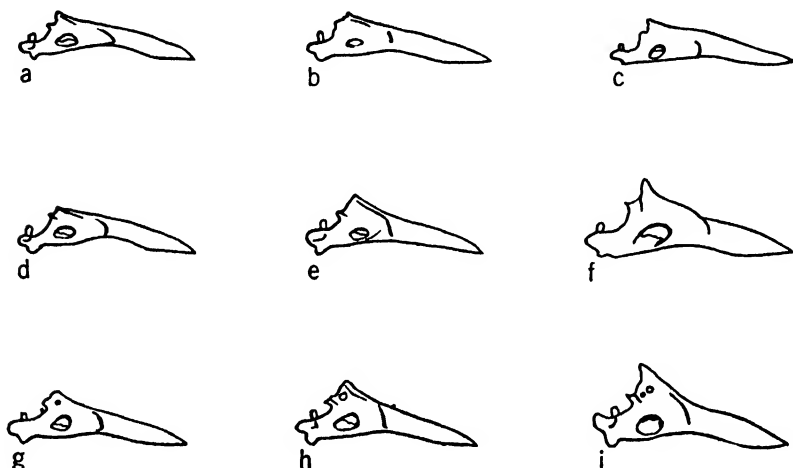


Fig. 8. Outline drawings ( $\times 1$ ) showing shape and size of ramus of individuals near average size in nine races of *Passerella iliaca*. a, *iliaca* no. 50742, Mus. Vert. Zool.; b, *unalaschcensis* coll. Calif. Acad. Sci.; c, *townsendi* no. 48999, Mus. Vert. Zool.; d, *fuliginosa* no. 48935, Mus. Vert. Zool.; e, *fulva* no. 48848, Mus. Vert. Zool.; f, *brevicauda* no. 48690, Mus. Vert. Zool.; g, *canescens* no. 51156, Mus. Vert. Zool.; h, *mariposae* no. 48720, Mus. Vert. Zool.; i, *stephensi* no. 50738, Mus. Vert. Zool.

of height of ramus for males of each sample by the mean of length of ramus in the same group: *iliaca* 0.27, *townsendi* 0.26, *fuliginosa* 0.26, *fulva* 0.34, *brevicauda* 0.39, *canescens* 0.31, *mariposae* M. 0.36, *mariposae* T. 0.36, *mariposae* S. 0.37, and *stephensi* 0.38. This bone shows more geographic variation than any other and, although there is a marked individual variation, there is less overlapping of values between samples from adjacent geographic regions than in the case of the other characters measured. It therefore seems plausible to conclude that, of the characters considered here, this one is of more diagnostic value than any other.

*Length and width of sternum.*—During the preparation of skeletons for study it was noted that in young birds the keel was one of the last parts of the skeleton to be deposited as bone. Only those birds that have been out of the nest for several days have fully developed keels.

TABLE 9  
VARIABILITY IN LENGTH OF STERNUM  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 5                   | 27 16      | 28 0    | 26 3    | 1 7   |                    |                                     |
| iliaca       | ♀   | 3                   | 24 60      | 24 8    | 24 2    | 6     |                    |                                     |
| townsendi    | ♂   | 8                   | 23 21      | 24 1    | 22 1    | 2 0   |                    |                                     |
| townsendi    | ♀   | 21                  | 22 18±0 12 | 24 3    | 21 0    | 3 3   | 83±0 09            | 3 74±0 39                           |
| fuliginosa   | ♂   | 15                  | 22 75      | 23 9    | 21 0    | 2 9   |                    |                                     |
| fuliginosa   | ♀   | 20                  | 21 66±0 09 | 22 6    | 20 6    | 2 0   | 57±0 06            | 2 65±0 28                           |
| fulva        | ♂   | 16                  | 22 18      | 23 0    | 21 1    | 1 9   |                    |                                     |
| fulva        | ♀   | 6                   | 20 96      | 21 8    | 20 0    | 1 8   |                    |                                     |
| brevicauda   | ♂   | 28                  | 22 90±0 08 | 23 7    | 21 6    | 2 1   | 63±0 06            | 2 74±0 25                           |
| brevicauda   | ♀   | 19                  | 21 87±0 11 | 23 1    | 20 4    | 2 7   | 74±0 08            | 3 39±0 37                           |
| canescens    | ♂   | 14                  | 22 32±0 10 | 23 3    | 21 6    | 1 7   | 57±0 07            | 2 54±0 32                           |
| canescens    | ♀   | 5                   | 20 66      | 21 4    | 20 1    | 1 3   |                    |                                     |
| mariposae M. | ♂   | 37                  | 22 27±0 07 | 23 9    | 21 0    | 2 8   | 63±0 05            | 2 82±0 22                           |
| mariposae M. | ♀   | 12                  | 21 38±0 12 | 22 3    | 20 0    | 2 3   | 63±0 08            | 2 96±0 38                           |
| mariposae T. | ♂   | 32                  | 22 31±0 08 | 23 5    | 20 9    | 2 6   | 68±0 06            | 3 05±0 26                           |
| mariposae T. | ♀   | 15                  | 21 20±0 14 | 22 5    | 19 8    | 2 7   | 80±0 09            | 3 78±0 47                           |
| mariposae S. | ♂   | 24                  | 22 82±0 08 | 23 6    | 21 6    | 2 0   | 55±0 05            | 2 43±0 24                           |
| mariposae S. | ♀   | 15                  | 21 54      | 22 2    | 20 3    | 1 9   |                    |                                     |
| stephensi    | ♂   | 25                  | 22 66±0 11 | 24 0    | 20 8    | 3 2   | 83±0 08            | 3 67±0 35                           |
| stephensi    | ♀   | 11                  | 21 59      | 23 0    | 20 4    | 2 6   |                    |                                     |

A considerable amount of individual variation exists in the shapes of various parts of the sternum. An extreme example of this is shown in figure V, an outline sketch of the sternum of no. 48735 (Mus. Vert. Zool.), which shows an instance in which both notches have been

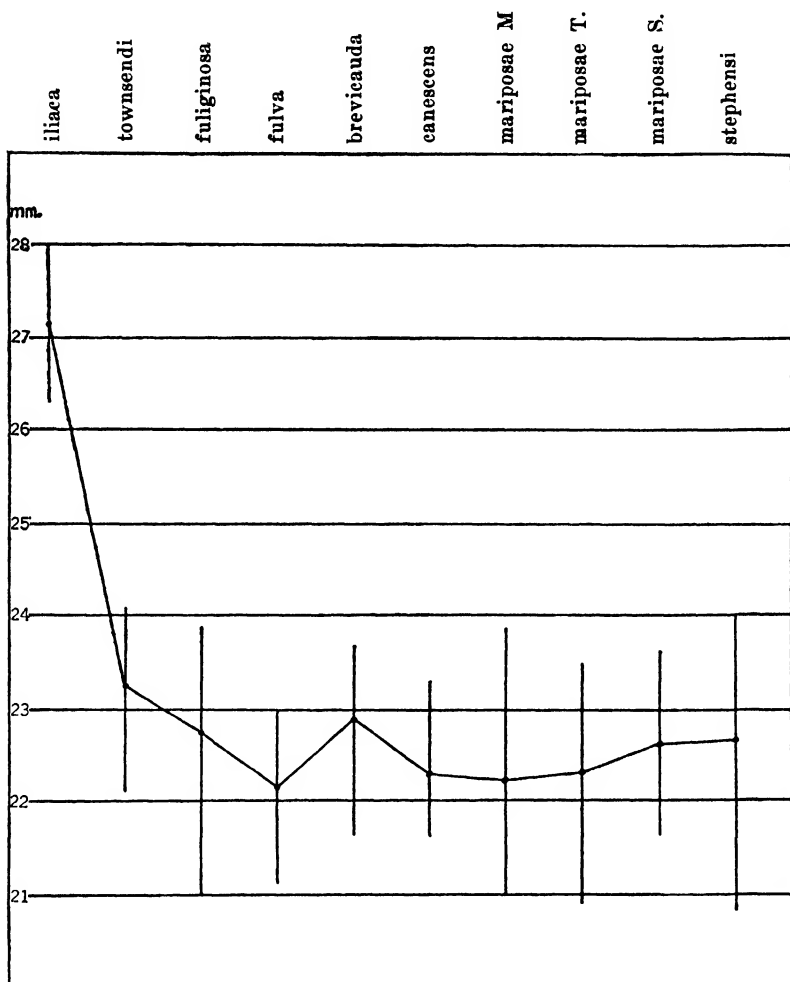


Fig. T. Diagram showing individual and geographic variation in length of sternum for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

entirely closed. This furnishes a concrete reminder of the possible dangers to be encountered in working with scanty material in avian osteology.

In every group except one in which variability coefficients were computed, the value for width of sternum is larger than for length

of sternum. This apparent greater variability may be due to mechanical difficulties in preparing and measuring the bones or it may represent an actual difference in the variability of these two measurements.

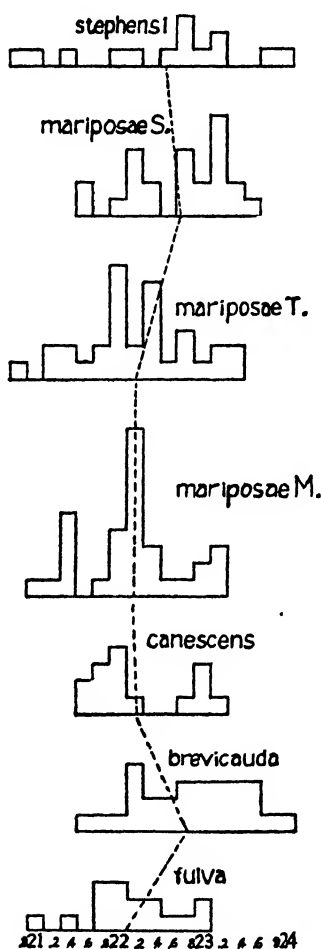


Fig. U. Histograms showing frequency distributions of values for length of sternum in seven samples of males.

Geographically there is little difference in these characters within the schistacea group but a surprisingly large gap separates *iliaca* from the others in respect to length of sternum. The longest sternum of *iliaca* measured twenty-eight millimeters while the longest of the schistacea group (*stephensi*) measured twenty-four millimeters. This

TABLE 10  
VARIABILITY IN WIDTH OF STERNUM  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean      | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|-----------|---------|---------|-------|--------------------|-------------------------------------|
| ilhaca       | ♂   | 5                   | 10.10     | 10.5    | 9.9     | 6     |                    |                                     |
| ilhaca       | ♀   | 3                   | 10.03     | 10.2    | 9.9     | 3     |                    |                                     |
| townsendi    | ♂   | 9                   | 10.07     | 10.6    | 9.3     | 1.3   |                    |                                     |
| townsendi    | ♀   | 23                  | 9.60±0.05 | 10.2    | 9.0     | 1.2   | 33±0.03            | 3.42±0.34                           |
| fuliginosa   | ♂   | 16                  | 9.79      | 10.4    | 9.2     | 1.2   |                    |                                     |
| fuliginosa   | ♀   | 19                  | 9.60±0.06 | 10.2    | 8.6     | 1.6   |                    |                                     |
| fulva        | ♂   | 16                  | 9.20      | 10.1    | 8.3     | 1.8   | 40±0.04            | 4.17±0.46                           |
| fulva        | ♀   | 7                   | 8.95      | 9.7     | 8.6     | 1.1   |                    |                                     |
| brevicauda   | ♂   | 29                  | 9.40±0.04 | 9.9     | 8.9     | 1.0   | 31±0.03            | 3.25±0.29                           |
| brevicauda   | ♀   | 19                  | 9.09±0.06 | 9.6     | 8.4     | 1.2   | 38±0.04            | 4.15±0.45                           |
| canescens    | ♂   | 16                  | 9.29±0.04 | 9.8     | 8.7     | 1.1   | 26±0.03            | 2.77±0.33                           |
| canescens    | ♀   | 5                   | 8.90      | 9.3     | 8.6     | 7     |                    |                                     |
| mariposae M. | ♂   | 38                  | 9.22±0.04 | 10.0    | 8.4     | 1.6   | 37±0.03            | 4.00±0.31                           |
| mariposae M. | ♀   | 14                  | 8.92±0.05 | 9.5     | 8.5     | 1.0   | 28±0.03            | 3.11±0.40                           |
| mariposae T. | ♂   | 31                  | 9.29±0.05 | 10.7    | 8.7     | 2.0   | 43±0.04            | 4.63±0.40                           |
| mariposae T. | ♀   | 15                  | 9.08±0.08 | 10.2    | 8.5     | 1.7   | 45±0.06            | 4.99±0.61                           |
| mariposae S. | ♂   | 24                  | 9.53±0.04 | 9.9     | 9.0     | 9     | 26±0.03            | 2.69±0.26                           |
| mariposae S. | ♀   | 16                  | 9.31      | 9.9     | 8.4     | 1.5   |                    |                                     |
| stephensi    | ♂   | 28                  | 9.43±0.06 | 10.1    | 8.4     | 1.6   | 47±0.04            | 5.02±0.45                           |
| stephensi    | ♀   | 10                  | 9.32      | 10.0    | 8.9     | 1.1   |                    |                                     |

contrast is especially emphasized when a comparison is made between these two races for height of ramus, in which character *iliaca* is only two-thirds as large as *stephensi*. The smallest sternum measured (female *mariposae* T.) was nineteen and eight-tenths millimeters long.

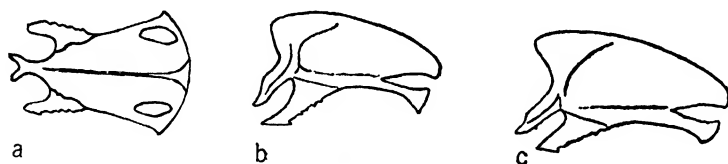


Fig. V. *a*, Abnormal sternum of *Passerella iliaca mariposae* ( $\times 1$ ) with notches closed; no. 48735, Mus. Vert. Zool. *b*, Side view of sternum of *P. i. mariposae* ( $\times 1$ ); no. 48733, Mus. Vert. Zool. *c*, Side view of sternum of *P. i. iliaca* ( $\times 1$ ); no. 54742, Mus. Vert. Zool.

*Length of pelvis*, for reasons previously explained, proved to be an unsatisfactory character for analysis. The uncertain phases of age and individual variation tended to obscure the tendency to vary geographically. Charts W and X, however, indicate that geographic variation in this character closely parallels that in width of sternum.

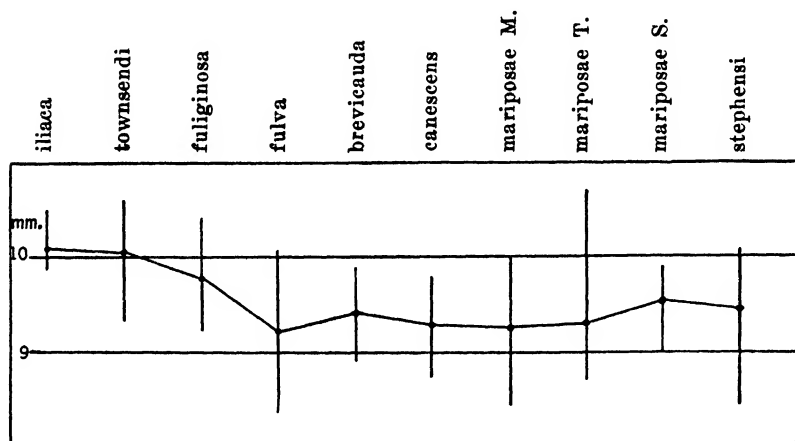


Fig. W. Diagram showing individual and geographic variation in width of sternum for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

*Lengths of femur, tibia, and tarsus.*—These three characters exhibit a surprising similarity in the various classes of variability. Although correlation coefficients were not computed, an examination of the tables and charts for these characters indicates that a high positive correlation exists between them. In each of the three bones

TABLE 11  
VARIABILITY IN LENGTH OF PELVIS  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| ilhaca       | ♂   | 2                   | 15 30      | 15 3    | 15 3    | 0     |                    |                                     |
| ilhaca       | ♀   | 3                   | 14 30      | 15 4    | 13 1    | 2 3   |                    |                                     |
| townsendi    | ♂   | 7                   | 15 21      | 16 0    | 14 7    | 1 3   |                    |                                     |
| townsendi    | ♀   | 20                  | 14 95±0 12 | 16 5    | 13 3    | 3 2   | 77±0 08            | 5 18±0 55                           |
| fuliginosa   | ♂   | 15                  | 15 04      | 16 3    | 13 4    | 2 9   |                    |                                     |
| fuliginosa   | ♀   | 19                  | 14 69±0 08 | 15 8    | 13 5    | 2 3   | 52±0 06            | 3 57±0 39                           |
| fulva        | ♂   | 16                  | 13 81      | 14 4    | 12 7    | 1 7   |                    |                                     |
| fulva        | ♀   | 7                   | 14 05      | 14 8    | 13 2    | 1 6   |                    |                                     |
| brevicauda   | ♂   | 30                  | 14 33±0 06 | 15 5    | 13 7    | 1 8   | 46±0 04            | 3 24±0 28                           |
| brevicauda   | ♀   | 16                  | 13 98±0 12 | 15 7    | 12 5    | 3 2   | 74±0 09            | 5 26±0 63                           |
| canescens    | ♂   | 16                  | 13 90±0 06 | 14 4    | 12 8    | 1 6   | 37±0 04            | 2 64±0 31                           |
| canescens    | ♀   | 7                   | 13 60      | 14 2    | 12 8    | 1 4   |                    |                                     |
| mariposae M. | ♂   | 34                  | 13 54±0 04 | 14 4    | 12 0    | 2 4   | 34±0 03            | 2 54±0 21                           |
| mariposae M. | ♀   | 15                  | 13 50±0 12 | 14 7    | 12 6    | 2 1   | 68±0 08            | 5 06±0 62                           |
| mariposae T. | ♂   | 29                  | 13 77±0 08 | 15 1    | 12 2    | 2 9   | 62±0 06            | 4 54±0 40                           |
| mariposae T. | ♀   | 14                  | 13 80±0 08 | 14 6    | 12 7    | 1 9   | 46±0 06            | 3 30±0 42                           |
| mariposae S. | ♂   | 19                  | 14 28±0 09 | 16 4    | 13 0    | 3 4   | 60±0 07            | 4 23±0 46                           |
| mariposae S. | ♀   | 14                  | 13 85      | 15 0    | 12 6    | 2 4   |                    |                                     |
| stephensi    | ♂   | 28                  | 14 08±0 09 | 15 3    | 12 4    | 2 9   | 70±0 06            |                                     |
| stephensi    | ♀   | 8                   | 13 61      | 15 2    | 12 6    | 2 6   |                    | 4 99±0 45                           |



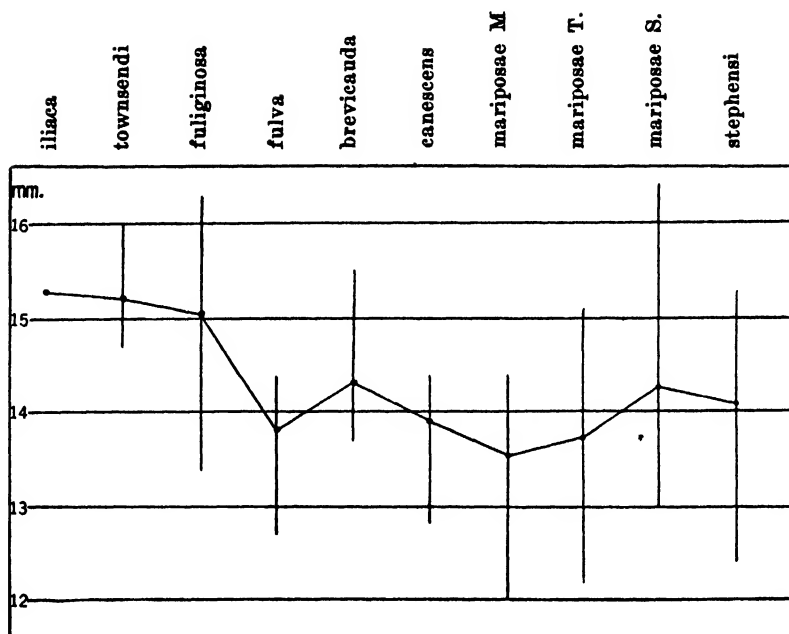


Fig. X. Diagram showing individual and geographic variation in length of pelvis for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

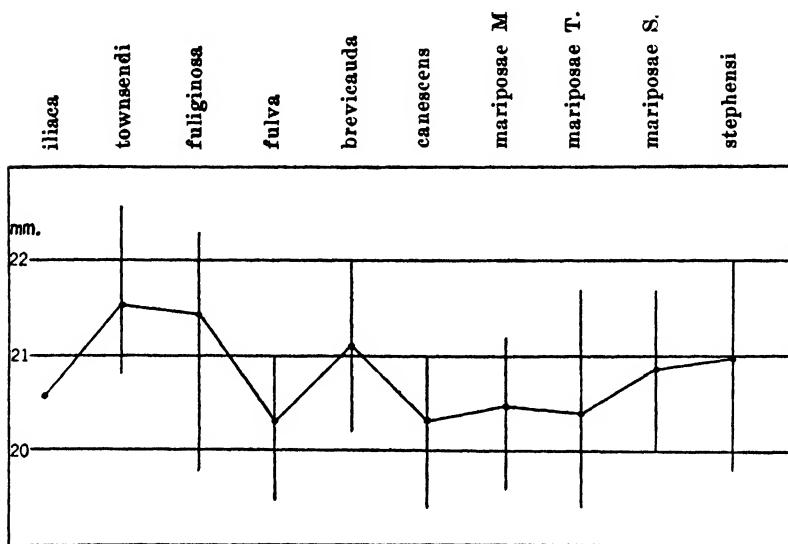


Fig. Y. Diagram showing individual and geographic variation in length of femur for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

TABLE 12  
VARIABILITY IN LENGTH OF TIBIAL  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| ulaca        | ♂   | 2                   | 20 60      | 20 6    | 20 6    | 0     |                    |                                     |
| ulaca        | ♀   | 2                   | 20 50      | 20 6    | 20 4    | 2     |                    |                                     |
| townsendi    | ♂   | 9                   | 21 57      | 22 6    | 20 8    | 1 8   |                    |                                     |
| townsendi    | ♀   | 22                  | 21 17±0 10 | 22 2    | 19 7    | 2 5   | 67±0 07            | 3 16±0 32                           |
| fuliginosa   | ♂   | 15                  | 21 44      | 22 3    | 19 8    | 2 5   |                    |                                     |
| fuliginosa   | ♀   | 18                  | 20 60±0 11 | 21 9    | 19 1    | 2 8   | 68±0 08            | 3 29±0 37                           |
| fulva        | ♂   | 16                  | 20 31      | 21 0    | 19 5    | 1 5   |                    |                                     |
| fulva        | ♀   | 7                   | 19 55      | 20 1    | 18 9    | 1 2   |                    |                                     |
| brevicauda   | ♂   | 31                  | 21 11±0 06 | 22 0    | 20 2    | 1 8   | 46±0 04            | 2 20±0 19                           |
| brevicauda   | ♀   | 17                  | 20 69±0 05 | 21 2    | 20 1    | 1 1   | 33±0 04            | 1 60±0 18                           |
| canescens    | ♂   | 15                  | 20 32±0 07 | 21 0    | 19 4    | 1 6   | 40±0 06            | 2 02±0 25                           |
| canescens    | ♀   | 7                   | 19 75      | 20 5    | 19 0    | 1 5   |                    |                                     |
| mariposae M. | ♂   | 35                  | 20 48±0 04 | 21 2    | 19 6    | 1 6   | 39±0 03            | 1 91±0 15                           |
| mariposae M. | ♀   | 15                  | 20 06±0 10 | 21 3    | 19 0    | 1 3   | 58±0 07            | 2 89±0 36                           |
| mariposae T. | ♂   | 33                  | 20 40±0 06 | 21 7    | 19 4    | 2 3   | 52±0 04            | 2 54±0 21                           |
| mariposae T. | ♀   | 17                  | 20 10±0 05 | 20 8    | 19 6    | 1 2   | 31±0 04            | 1 56±0 18                           |
| mariposae S. | ♂   | 21                  | 20 84±0 07 | 21 7    | 20 0    | 1 7   | 48±0 05            | 2 29±0 24                           |
| mariposae S. | ♀   | 16                  | 20 33      | 21 1    | 19 3    | 1 8   |                    |                                     |
| stephensi    | ♂   | 27                  | 20 97±0 07 | 22 0    | 19 8    | 2 2   | 53±0 05            | 2 40±0 22                           |
| stephensi    | ♀   | 12                  | 20 51      | 21 3    | 19 4    | 1 9   |                    |                                     |

TABLE 13  
VARIABILITY IN LENGTH OF TIBIA (TIBIO-TARSUS)  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| ilhaca       | ♂   | 2                   | 35.35      | 35.6    | 35.1    | 5     |                    |                                     |
| ilhaca       | ♀   | 3                   | 34.80      | 35.1    | 34.4    | 7     |                    |                                     |
| townsendi    | ♂   | 9                   | 36.21      | 37.8    | 35.0    | 2.8   |                    |                                     |
| townsendi    | ♀   | 19                  | 35.85±0.15 | 37.5    | 33.6    | 3.9   | 96±0.11            | 2.69±0.29                           |
| fuliginosa   | ♂   | 16                  | 36.23      | 37.7    | 35.0    | 2.7   |                    |                                     |
| fuliginosa   | ♀   | 19                  | 35.34±0.19 | 37.2    | 31.9    | 5.3   | 1.25±0.14          | 3.54±0.39                           |
| fulva        | ♂   | 17                  | 34.08      | 35.3    | 32.9    | 2.4   |                    |                                     |
| fulva        | ♀   | 6                   | 33.11      | 34.5    | 32.0    | 2.5   |                    |                                     |
| brevicauda   | ♂   | 24                  | 35.51±0.09 | 36.9    | 34.2    | 2.7   | 66±0.06            | 1.87±0.18                           |
| brevicauda   | ♀   | 18                  | 34.78±0.18 | 36.7    | 32.6    | 4.1   | 1.15±0.13          | 3.31±0.37                           |
| canescens    | ♂   | 15                  | 34.11±0.14 | 35.8    | 32.7    | 3.1   | 80±0.10            | 2.34±0.29                           |
| canescens    | ♀   | 7                   | 33.48      | 35.0    | 31.9    | 3.1   |                    |                                     |
| mariposae M. | ♂   | 35                  | 34.16±0.10 | 35.5    | 31.3    | 4.2   | 87±0.07            | 2.54±0.20                           |
| mariposae M. | ♀   | 13                  | 34.10±0.13 | 35.2    | 32.7    | 2.5   | 70±0.09            | 2.06±0.27                           |
| mariposae T. | ♂   | 32                  | 34.41±0.09 | 36.3    | 32.7    | 3.6   | 76±0.06            | 2.21±0.19                           |
| mariposae T. | ♀   | 14                  | 33.70±0.14 | 35.1    | 32.0    | 3.1   | 80±0.10            | 2.38±0.30                           |
| mariposae S. | ♂   | 25                  | 34.70±0.11 | 36.6    | 33.2    | 3.4   | 81±0.08            | 2.33±0.22                           |
| mariposae S. | ♀   | 14                  | 34.08      | 35.8    | 32.4    | 3.4   |                    |                                     |
| stephensi    | ♂   | 32                  | 35.19±0.11 | 36.7    | 33.3    | 3.4   | 89±0.07            | 2.52±0.21                           |
| stephensi    | ♀   | 10                  | 34.25      | 36.0    | 32.2    | 3.8   |                    |                                     |

the series of female *fuliginosa* shows the greatest range and in each instance the range is within 1 per cent of 15 per cent of the mean value for that character.

If this study were to be continued it would seem desirable to keep on making measurements of only one of these bones. Individual

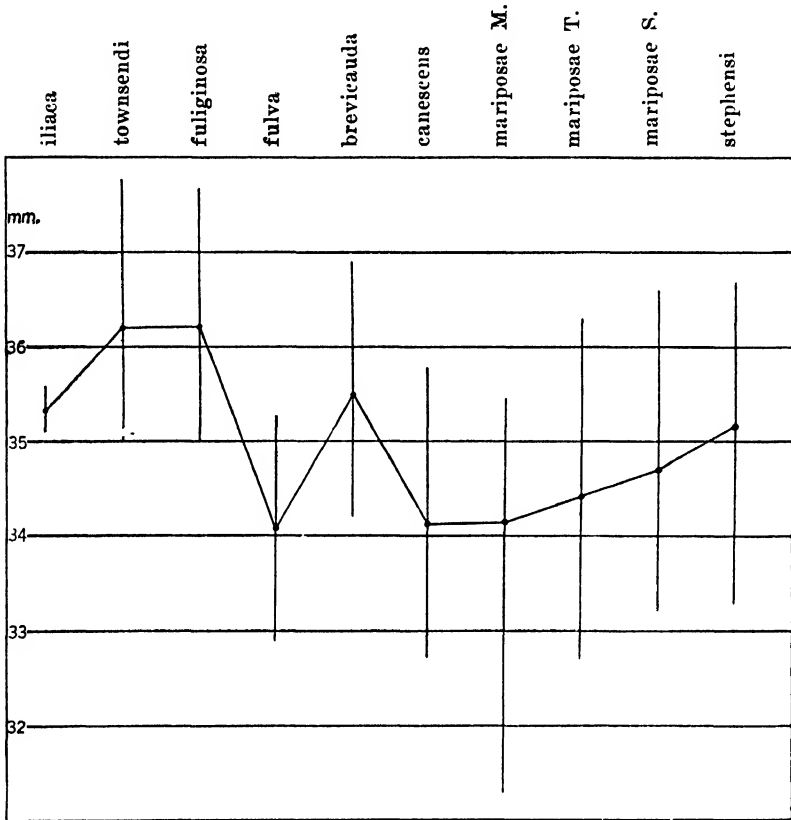


Fig. Z. Diagram showing individual and geographic variation in length of tibia (tibio-tarsus) for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

variation in these characters is so small that the geographic differences, even though small, proved to be significant in several instances.

*Lengths of humerus, radius, and ulna* comprise another set of characters similar to the one just described. In this set there is less individual variation; in fact, the length of humerus is the least variable, individually, of all the characters used. It may be well to point out here that this complex of characters closely resembles, in its

TABLE 14  
VARIABILITY IN LENGTH OF TARSUS (TARSO-METATARSUS)  
Measurements in millimeters

| Sample              | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|---------------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| <i>iliaca</i>       | ♂   | 2                   | 24.50      | 24.5    | 24.5    | 0     |                    |                                     |
| <i>ihaca</i>        | ♀   | 2                   | 24.35      | 24.5    | 24.2    | 3     |                    |                                     |
| <i>townsendi</i>    | ♂   | 10                  | 25.20      | 26.2    | 24.0    | 2.2   |                    |                                     |
| <i>townsendi</i>    | ♀   | 21                  | 25.17±0.10 | 26.2    | 23.7    | 2.5   | 66±0.07            | 2.60±0.27                           |
| <i>fuliginosa</i>   | ♂   | 16                  | 25.37      | 26.4    | 23.8    | 2.6   |                    |                                     |
| <i>fuliginosa</i>   | ♀   | 19                  | 24.63±0.14 | 25.8    | 22.1    | 3.7   | 88±0.10            | 3.59±0.39                           |
| <i>fulva</i>        | ♂   | 17                  | 24.04      | 24.6    | 22.9    | 1.7   |                    |                                     |
| <i>fulva</i>        | ♀   | 7                   | 23.34      | 23.9    | 22.4    | 1.5   |                    |                                     |
| <i>brevicauda</i>   | ♂   | 31                  | 25.03±0.08 | 26.9    | 23.7    | 3.2   | 69±0.06            | 2.77±0.23                           |
| <i>brevicauda</i>   | ♀   | 19                  | 24.52±0.10 | 26.2    | 23.2    | 3.0   | 67±0.07            | 2.72±0.30                           |
| <i>canescens</i>    | ♂   | 15                  | 23.91±0.12 | 25.5    | 22.9    | 2.6   | 67±0.08            | 2.80±0.34                           |
| <i>canescens</i>    | ♀   | 7                   | 23.24      | 24.4    | 22.1    | 2.3   |                    |                                     |
| <i>mariposae</i> M. | ♂   | 38                  | 24.16±0.07 | 25.5    | 22.0    | 3.5   | 67±0.05            | 2.78±0.21                           |
| <i>mariposae</i> M. | ♀   | 13                  | 23.79±0.09 | 24.4    | 22.6    | 1.8   | 50±0.07            | 2.09±0.28                           |
| <i>mariposae</i> T. | ♂   | 35                  | 24.26±0.08 | 26.3    | 23.1    | 3.2   | 71±0.05            | 2.91±0.23                           |
| <i>mariposae</i> T. | ♀   | 17                  | 23.99±0.11 | 25.0    | 22.3    | 2.7   | 65±0.08            | 2.73±0.32                           |
| <i>mariposae</i> S. | ♂   | 25                  | 24.66±0.08 | 26.1    | 23.4    | 2.7   | 63±0.06            | 2.55±0.25                           |
| <i>mariposae</i> S. | ♀   | 15                  | 24.26      | 26.2    | 22.8    | 3.4   |                    |                                     |
| <i>stephensi</i>    | ♂   | 32                  | 24.96±0.07 | 26.4    | 23.7    | 2.7   | 57±0.05            | 2.29±0.19                           |
| <i>stephensi</i>    | ♀   | 12                  | 24.44      | 25.8    | 23.2    | 2.6   |                    |                                     |

geographic behavior, the arrangement of length of sternum in the various groups. However, in that character *iliaca* is set off much farther from the rest than in any of the characters of the group now being considered.

*Lengths of coracoid, scapula, and furcula* are characters which behave so similarly as to merit treatment together. Of these, the length

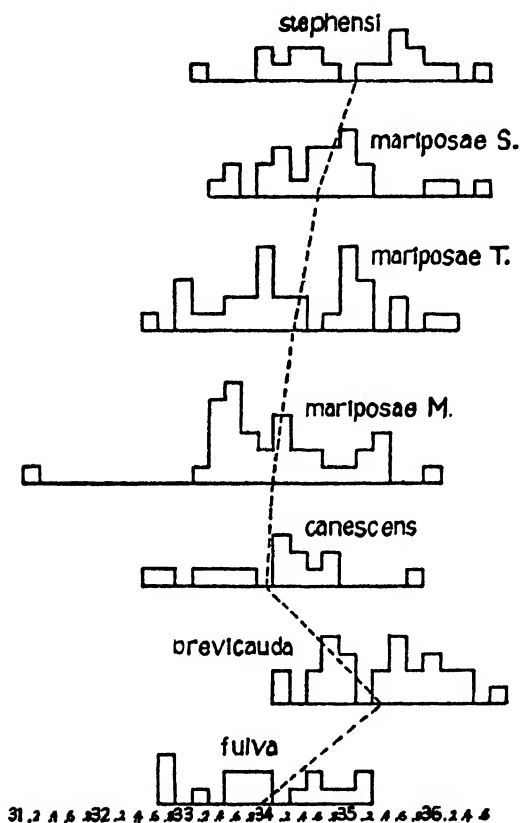


Fig. AA. Histograms showing frequency distributions of values for length of tibia (tibio-tarsus) in seven samples of males.

of coracoid shows less individual variation than the other two, chiefly because there is less mechanical error induced in the preparation and measurement of that bone. In one specimen (*undulascensis*) the coracoid is fused to the sternum, a condition apparently pathological.

The scapula is another bone which does not assume its final form, in bone, for several weeks after the birds leave the nest. Several

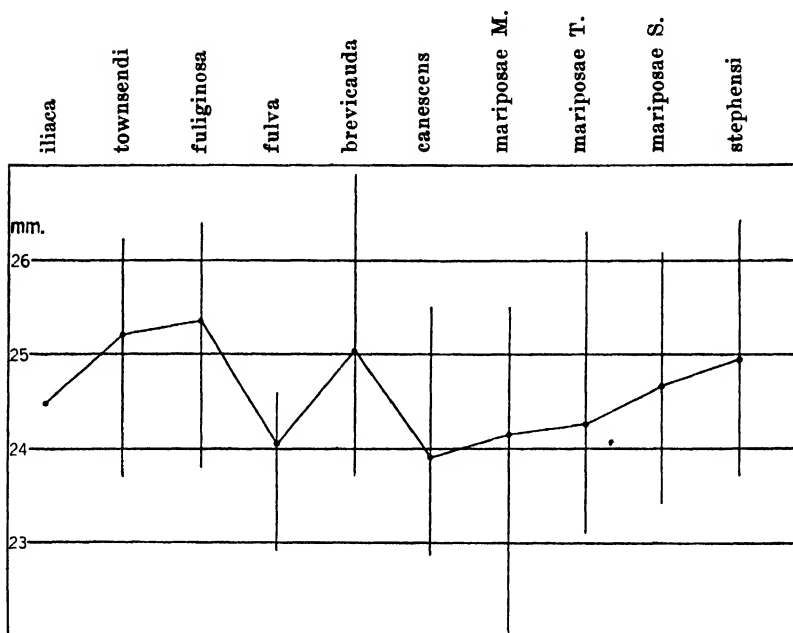


Fig. BB. Diagram showing individual and geographic variation in length of tarsus (tarso-metatarsus) for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

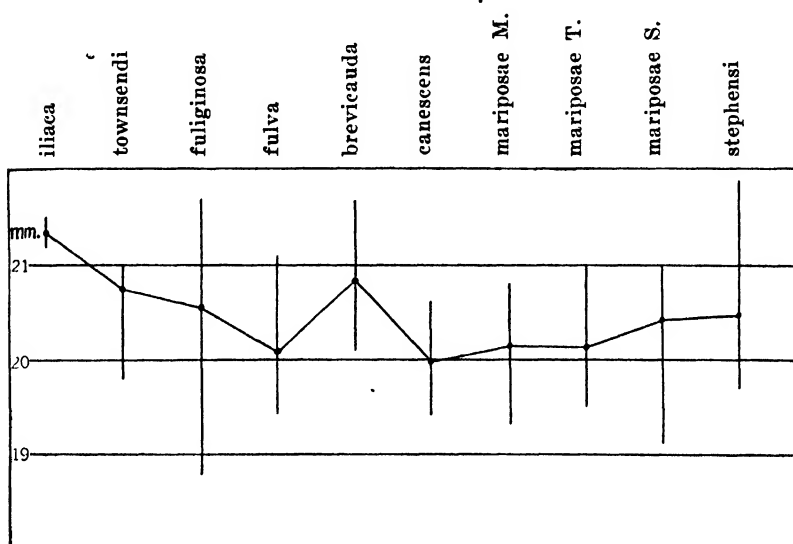


Fig. CC. Diagram showing individual and geographic variation in length of humerus for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

TABLE 15  
VARIABILITY IN LENGTH OF HUMERUS  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 2                   | 21 35      | 21 5    | 21 2    | 3     |                    |                                     |
| iliaca       | ♀   | 3                   | 21 73      | 21 1    | 20 2    | 9     |                    |                                     |
| townsendi    | ♂   | 9                   | 20 74      | 21 0    | 19 8    | 1 2   |                    |                                     |
| townsendi    | ♀   | 20                  | 20 04±0 07 | 20 9    | 19 1    | 1 8   | 47±0 05            | 2 36±0 25                           |
| fuliginosa   | ♂   | 15                  | 20 54      | 21 7    | 18 8    | 2 9   |                    |                                     |
| fuliginosa   | ♀   | 19                  | 19 65±0 08 | 20 4    | 18 1    | 2 3   | 54±0 06            | 2 76±0 30                           |
| fulva        | ♂   | 17                  | 20 07      | 21 1    | 19 4    | 1 7   |                    |                                     |
| fulva        | ♀   | 7                   | 19 03      | 19 6    | 18 4    | 1 2   |                    |                                     |
| brevicauda   | ♂   | 31                  | 20 84±0 04 | 21 7    | 20 1    | 1 6   | 37±0 03            | 1 77±0 15                           |
| brevicauda   | ♀   | 16                  | 20 16±0 07 | 21 0    | 19 4    | 1 6   | 40±0 05            | 1 97±0 23                           |
| canescens    | ♂   | 15                  | 19 99±0 08 | 20 6    | 19 4    | 1 2   | 35±0 04            | 1 77±0 22                           |
| canescens    | ♀   | 5                   | 19 48      | 20 1    | 18 8    | 1 3   |                    |                                     |
| mariposae M. | ♂   | 36                  | 20 17±0 04 | 20 8    | 19 3    | 1 5   | 33±0 03            | 1 65±0 13                           |
| mariposae M. | ♀   | 14                  | 19 51±0 08 | 20 1    | 18 7    | 1 4   | 44±0 06            | 2 20±0 28                           |
| mariposae T. | ♂   | 34                  | 20 12±0 05 | 21 0    | 19 5    | 1 5   | 42±0 03            | 2 08±0 17                           |
| mariposae T. | ♀   | 17                  | 19 53±0 05 | 20 2    | 19 1    | 1 1   | 31±0 04            | 1 57±0 18                           |
| mariposae S. | ♂   | 22                  | 20 41±0 06 | 21 0    | 19 1    | 1 9   | 41±0 04            | 2 00±0 20                           |
| mariposae S. | ♀   | 16                  | 19 78      | 20 8    | 19 1    | 1 7   |                    |                                     |
| stephensi    | ♂   | 26                  | 20 49±0 07 | 21 9    | 19 7    | 2 2   | 57±0 05            | 2 76±0 26                           |
| stephensi    | ♀   | 11                  | 19 73      | 20 6    | 18 8    | 1 8   |                    |                                     |



instances were noted in which this bone was malformed, apparently as a result of being broken or injured during its growth. The same condition was noted in several furculae. In this bone individual variation and to some degree geographic variation consisted in differing shapes and sizes of the hypocleideum.

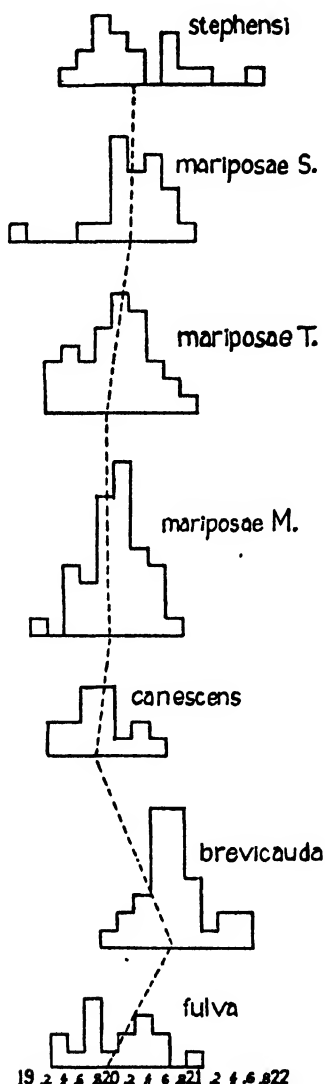


Fig. DD. Histograms showing frequency distributions of values for length of humerus in seven samples of males.

TABLE 16  
VARIABILITY IN LENGTH OF RADIUS  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 2                   | 21 90      | 21 9    | 21 9    | 0     |                    |                                     |
| iliaca       | ♀   | 3                   | 21 13      | 21 3    | 21 0    | 3     |                    |                                     |
| townsendi    | ♂   | 10                  | 20 69      | 21 4    | 19 7    | 1 7   |                    |                                     |
| townsendi    | ♀   | 22                  | 19 81±0 08 | 20 8    | 18 8    | 2 0   | 52±0 05            | 2 64±0 27                           |
| fuliginosa   | ♂   | 16                  | 20 24      | 21 9    | 18 3    | 3 6   |                    |                                     |
| fuliginosa   | ♀   | 19                  | 19 35±0 11 | 20 2    | 17 9    | 2 4   |                    |                                     |
| fulva        | ♂   | 17                  | 20 24      | 20 8    | 19 6    | 1 2   | 71±0 08            | 3 64±0 40                           |
| fulva        | ♀   | 7                   | 18 97      | 19 7    | 18 4    | 1 3   |                    |                                     |
| brevicauda   | ♂   | 31                  | 21 08±0 05 | 21 9    | 20 2    | 1 7   | 41±0 04            | 1 96±0 17                           |
| brevicauda   | ♀   | 19                  | 19 84±0 06 | 20 5    | 18 8    | 1 7   | 39±0 04            | 1 99±0 22                           |
| canescens    | ♂   | 15                  | 20 18±0 07 | 20 9    | 19 2    | 1 7   | 41±0 05            | 2 01±0 25                           |
| canescens    | ♀   | 6                   | 19 21      | 19 9    | 18 5    | 1 4   |                    |                                     |
| mariposae M. | ♂   | 37                  | 20 36±0 05 | 21 6    | 19 0    | 2 6   | 43±0 03            | 2 11±0 16                           |
| mariposae M. | ♀   | 15                  | 19 35±0 07 | 20 2    | 18 6    | 1 6   | 41±0 05            | 2 04±0 25                           |
| mariposae T. | ♂   | 36                  | 20 30±0 06 | 21 3    | 19 0    | 2 3   | 53±0 04            | 2 76±0 22                           |
| mariposae T. | ♀   | 18                  | 19 35±0 09 | 20 5    | 18 2    | 2 3   | 54±0 06            | 2 82±0 32                           |
| mariposae S. | ♂   | 22                  | 20 68±0 05 | 21 5    | 20 0    | 1 5   | 37±0 04            | 1 77±0 18                           |
| mariposae S. | ♀   | 15                  | 19 56      | 21 1    | 18 8    | 2 3   |                    |                                     |
| stephensi    | ♂   | 26                  | 20 71±0 07 | 21 8    | 19 8    | 2 0   |                    |                                     |
| stephensi    | ♀   | 12                  | 19 50      | 20 7    | 18 1    | 2 6   | 54±0 05            | 2 61±0 24                           |

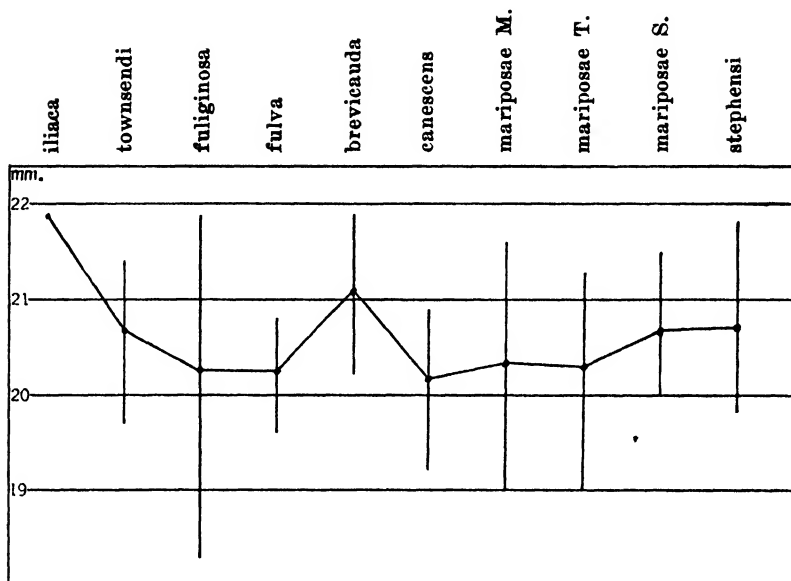


Fig. EE. Diagram showing individual and geographic variation in length of radius for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

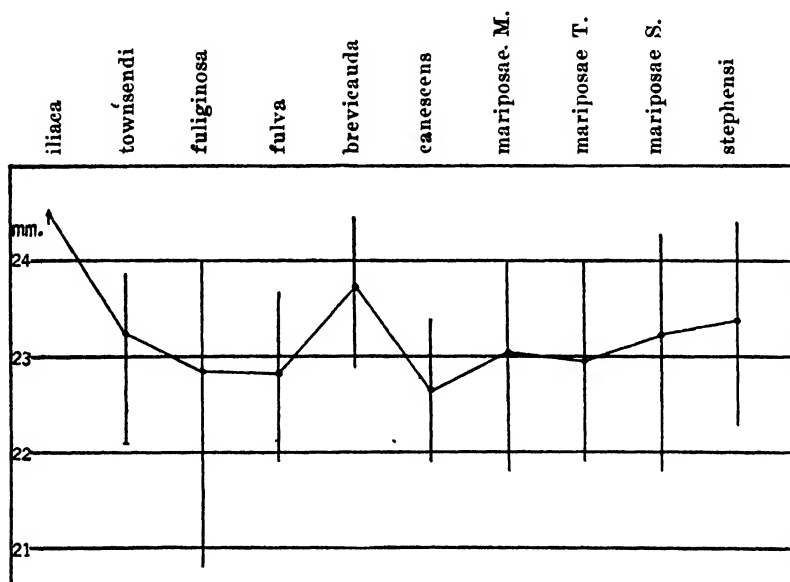


Fig. FF. Diagram showing individual and geographic variation in length of ulna for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

TABLE 17  
VARIABILITY IN LENGTH OF ULNA  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 2                   | 24.45      | 24.5    | 24.4    | 1     |                    |                                     |
| iliaca       | ♀   | 3                   | 23.80      | 24.2    | 23.5    | 7     |                    |                                     |
| townsendi    | ♂   | 10                  | 23.24      | 23.9    | 22.1    | 1.8   |                    |                                     |
| townsendi    | ♀   | 22                  | 22.39±0.09 | 23.7    | 21.2    | 2.5   | 65±0.07            | 2.90±0.29                           |
| fuliginosa   | ♂   | 16                  | 22.84      | 24.0    | 20.8    | 3.2   |                    |                                     |
| fuliginosa   | ♀   | 20                  | 21.83±0.12 | 22.7    | 20.0    | 2.7   | 77±0.08            | 3.52±0.38                           |
| fulva        | ♂   | 17                  | 22.81      | 23.7    | 21.9    | 1.8   |                    |                                     |
| fulva        | ♀   | 6                   | 21.42      | 22.1    | 20.9    | 1.2   |                    |                                     |
| brevicauda   | ♂   | 31                  | 23.74±0.05 | 24.4    | 22.9    | 1.5   | 39±0.03            | 1.66±0.14                           |
| brevicauda   | ♀   | 17                  | 22.59±0.06 | 23.3    | 21.5    | 1.8   | 38±0.04            | 1.70±0.20                           |
| canescens    | ♂   | 15                  | 22.73±0.07 | 23.4    | 21.9    | 1.5   | 40±0.05            | 1.77±0.22                           |
| canescens    | ♀   | 5                   | 21.60      | 22.5    | 20.9    | 1.6   |                    |                                     |
| mariposae M. | ♂   | 37                  | 23.07±0.05 | 24.0    | 21.8    | 2.2   | 42±0.03            | 1.82±0.14                           |
| mariposae M. | ♀   | 15                  | 21.96±0.08 | 22.9    | 21.0    | 1.9   | 45±0.06            | 2.06±0.25                           |
| mariposae T. | ♂   | 34                  | 22.97±0.07 | 24.0    | 21.9    | 2.1   | 58±0.05            | 2.53±0.21                           |
| mariposae T. | ♀   | 18                  | 21.91±0.08 | 23.0    | 20.9    | 2.1   | 48±0.05            | 2.20±0.25                           |
| mariposae S. | ♂   | 21                  | 23.21±0.07 | 24.3    | 21.8    | 2.5   | 48±0.05            | 2.06±0.21                           |
| mariposae S. | ♀   | 15                  | 22.20      | 23.8    | 21.1    | 2.7   |                    |                                     |
| stephensi    | ♂   | 25                  | 23.39±0.08 | 24.4    | 22.3    | 2.1   | 59±0.06            | 2.54±0.24                           |
| stephensi    | ♀   | 12                  | 22.15      | 23.3    | 21.0    | 2.3   |                    |                                     |

TABLE 18  
VARIABILITY IN LENGTH OF CORACOID  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 2                   | 18 90      | 19 2    | 18 6    | 6     |                    |                                     |
| iliaca       | ♀   | 3                   | 18 50      | 19 0    | 18 1    | 9     |                    |                                     |
| townsendi    | ♂   | 8                   | 18 17      | 18 7    | 17 3    | 1 4   |                    |                                     |
| townsendi    | ♀   | 21                  | 17 31±0 08 | 18 3    | 16 3    | 2 0   | 53±0 06            | 3 08±0 32                           |
| fuliginosa   | ♂   | 15                  | 17 88      | 18 9    | 16 4    | 2 5   |                    |                                     |
| fuliginosa   | ♀   | 20                  | 16 92±0 12 | 17 6    | 15 4    | 2 2   | 78±0 08            | 4 62±0 49                           |
| fulva        | ♂   | 16                  | 17 35      | 17 7    | 16 7    | 1 0   |                    |                                     |
| fulva        | ♀   | 7                   | 16 50      | 17 1    | 15 9    | 1 2   |                    |                                     |
| brevicauda   | ♂   | 29                  | 18 25±0 05 | 19 0    | 17 5    | 1 5   | 40±0 04            | 2 18±0 19                           |
| brevicauda   | ♀   | 18                  | 17 49±0 06 | 18 3    | 16 5    | 1 8   | 39±0 04            | 2 22±0 25                           |
| canescens    | ♂   | 15                  | 17 24±0 08 | 18 0    | 16 2    | 1 8   | 49±0 06            | 2 81±0 35                           |
| canescens    | ♀   | 7                   | 16 44      | 17 3    | 15 4    | 1 9   |                    |                                     |
| mariposae M. | ♂   | 37                  | 17 54±0 05 | 18 5    | 16 7    | 1 8   | 41±0 03            | 2 33±0 18                           |
| mariposae M. | ♀   | 14                  | 16 95±0 09 | 17 5    | 15 7    | 1 8   | 48±0 06            | 2 83±0 36                           |
| mariposae T. | ♂   | 35                  | 17 46±0 06 | 18 8    | 15 7    | 3 1   | 53±0 04            | 3 03±0 24                           |
| mariposae T. | ♀   | 16                  | 16 75±0 07 | 17 4    | 16 1    | 1 3   | 39±0 05            | 2 32±0 28                           |
| mariposae S. | ♂   | 24                  | 17 80±0 06 | 18 5    | 16 2    | 2 3   | 44±0 04            | 2 44±0 24                           |
| mariposae S. | ♀   | 15                  | 17 04      | 17 7    | 16 3    | 1 4   |                    |                                     |
| stephensi    | ♂   | 31                  | 17 73±0 07 | 19 2    | 16 7    | 2 5   | 54±0 05            | 3 03±0 26                           |
| stephensi    | ♀   | 11                  | 16 84      | 17 8    | 15 9    | 1 9   |                    |                                     |

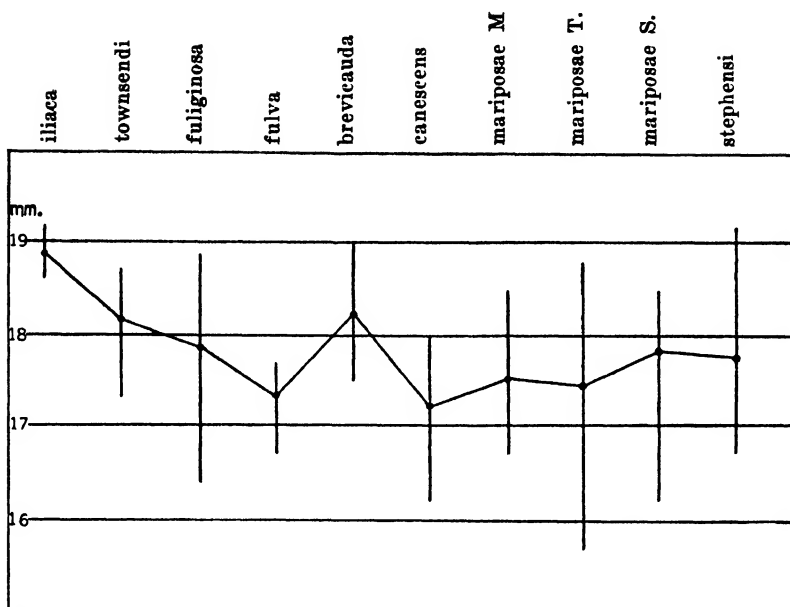


Fig. GG. Diagram showing individual and geographic variation in length of coracoid for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

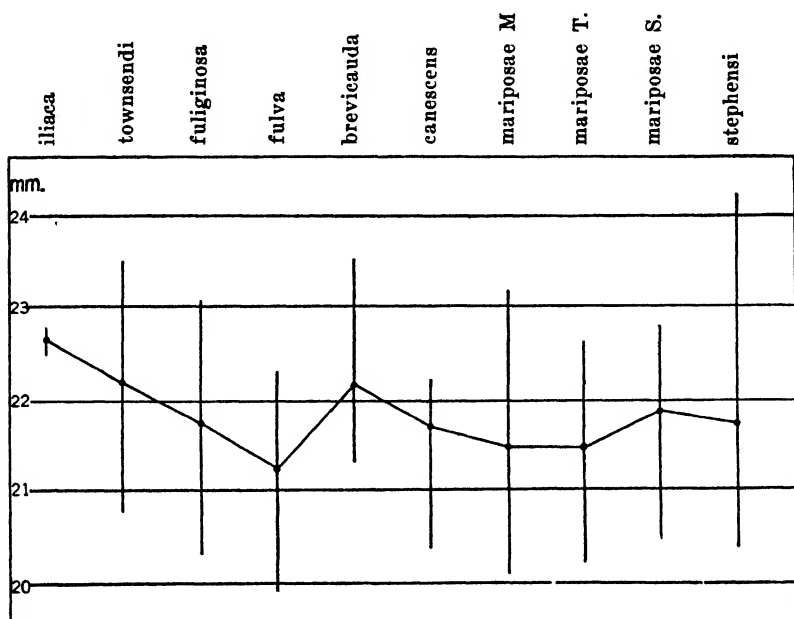


Fig. HH. Diagram showing individual and geographic variation in length of scapula for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

TABLE 19  
VARIABILITY IN LENGTH OF SCAPULA  
Measurements in millimeters

| Sample              | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|---------------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| <i>iliaca</i>       | ♂   | 2                   | 22.65      | 22.8    | 22.5    | 3     |                    |                                     |
| <i>iliaca</i>       | ♀   | 2                   | 21.60      | 22.4    | 20.8    | 1.6   |                    |                                     |
| <i>townsendi</i>    | ♂   | 10                  | 22.19      | 23.5    | 20.8    | 2.7   |                    |                                     |
| <i>townsendi</i>    | ♀   | 21                  | 21.10±0.10 | 22.4    | 19.8    | 2.6   | 69±0.07            | 3.25±0.34                           |
| <i>fuliginosa</i>   | ♂   | 16                  | 21.73      | 23.1    | 20.3    | 2.8   |                    |                                     |
| <i>fuliginosa</i>   | ♀   | 19                  | 20.70±0.09 | 21.7    | 19.2    | 2.5   | 57±0.06            | 2.76±0.30                           |
| <i>fulva</i>        | ♂   | 17                  | 21.26      | 22.3    | 19.9    | 2.4   |                    |                                     |
| <i>fulva</i>        | ♀   | 7                   | 20.24      | 21.9    | 19.0    | 1.9   |                    |                                     |
| <i>brevicauda</i>   | ♂   | 31                  | 22.17±0.06 | 23.5    | 21.3    | 2.2   | 52±0.04            | 2.36±0.20                           |
| <i>brevicauda</i>   | ♀   | 19                  | 21.48±0.11 | 22.8    | 20.1    | 2.7   | 73±0.08            | 3.38±0.37                           |
| <i>canescens</i>    | ♂   | 15                  | 21.69±0.09 | 22.2    | 20.4    | 1.8   | 52±0.06            | 2.39±0.29                           |
| <i>canescens</i>    | ♀   | 6                   | 20.43      | 21.0    | 19.5    | 1.5   |                    |                                     |
| <i>mariposae</i> M. | ♂   | 36                  | 21.43±0.07 | 23.2    | 20.1    | 3.1   | 59±0.05            | 2.77±0.22                           |
| <i>mariposae</i> M. | ♀   | 14                  | 20.53±0.12 | 21.3    | 19.2    | 2.1   | 66±0.08            | 3.24±0.41                           |
| <i>mariposae</i> T. | ♂   | 33                  | 21.45±0.07 | 22.6    | 20.2    | 2.4   | 60±0.05            | 2.73±0.23                           |
| <i>mariposae</i> T. | ♀   | 17                  | 20.49±0.13 | 22.3    | 18.9    | 3.4   | 81±0.09            | 3.97±0.46                           |
| <i>mariposae</i> S. | ♂   | 24                  | 21.91±0.08 | 22.8    | 20.5    | 2.3   | 57±0.06            | 2.60±0.25                           |
| <i>mariposae</i> S. | ♀   | 15                  | 20.97      | 22.1    | 20.1    | 2.0   |                    |                                     |
| <i>stephensi</i>    | ♂   | 31                  | 21.77±0.09 | 24.2    | 20.4    | 3.8   | 77±0.07            | 3.53±0.30                           |
| <i>stephensi</i>    | ♀   | 12                  | 21.07      | 22.4    | 19.4    | 3.0   |                    |                                     |

TABLE 20  
VARIABILITY IN LENGTH OF FURCULA  
Measurements in millimeters

| Sample       | Sex | Number of specimens | Mean       | Maximum | Minimum | Range | Standard deviation | Coefficient of variation (per cent) |
|--------------|-----|---------------------|------------|---------|---------|-------|--------------------|-------------------------------------|
| iliaca       | ♂   | 2                   | 17.05      | 17.1    | 17.0    | 1     |                    |                                     |
| iliaca       | ♀   | 3                   | 17.20      | 17.3    | 17.1    | 2     |                    |                                     |
| townsendi    | ♂   | 8                   | 16.63      | 17.3    | 16.1    | 1 2   |                    |                                     |
| townsendi    | ♀   | 21                  | 16.34±0.10 | 17.5    | 15.3    | 2 2   | 66±0.07            | 4.05±0.42                           |
| fuliginosa   | ♂   | 16                  | 16.26      | 17.2    | 15.3    | 1 9   |                    |                                     |
| fuliginosa   | ♀   | 18                  | 15.83±0.09 | 16.9    | 14.6    | 2 3   | 58±0.07            | 3.67±0.41                           |
| fulva        | ♂   | 17                  | 15.99      | 16.8    | 14.9    | 1 9   |                    |                                     |
| fulva        | ♀   | 7                   | 15.31      | 16.1    | 14.6    | 1 5   |                    |                                     |
| brevicauda   | ♂   | 30                  | 16.40±0.08 | 18.2    | 15.2    | 3 0   | 65±0.06            | 3.99±0.35                           |
| brevicauda   | ♀   | 18                  | 16.07±0.07 | 16.6    | 14.8    | 1 8   | 45±0.05            | 2.81±0.32                           |
| canescens    | ♂   | 15                  | 15.91±0.12 | 17.2    | 14.5    | 2 7   | 68±0.08            | 4.24±0.52                           |
| canescens    | ♀   | 7                   | 15.40      | 16.2    | 14.3    | 1 9   |                    |                                     |
| mariposae M. | ♂   | 36                  | 15.65±0.06 | 17.3    | 14.8    | 2 5   | 56±0.04            | 3.57±0.28                           |
| mariposae M. | ♀   | 15                  | 15.29±0.12 | 16.6    | 14.2    | 2 4   | 69±0.08            | 4.51±0.55                           |
| mariposae T. | ♂   | 32                  | 15.90±0.08 | 17.2    | 14.5    | 2 7   | 65±0.05            | 4.06±0.34                           |
| mariposae T. | ♀   | 15                  | 15.58±0.07 | 16.0    | 14.8    | 1 2   | 40±0.05            | 2.58±0.32                           |
| mariposae S. | ♂   | 23                  | 16.08±0.07 | 17.1    | 15.3    | 1 8   | 51±0.05            | 3.17±0.31                           |
| mariposae S. | ♀   | 16                  | 15.78      | 16.5    | 15.0    | 1 5   |                    |                                     |
| stephensi    | ♂   | 29                  | 15.85±0.08 | 17.6    | 14.7    | 2 9   | 65±0.06            | 4.09±0.36                           |
| stephensi    | ♀   | 10                  | 15.88      | 16.8    | 14.5    | 2 3   |                    |                                     |



## CORRELATION WITH VARIATION IN EXTERNAL CHARACTERS

A close study of the various graphical presentations of the measurements made shows that in every character measured there are differences in absolute size which may be correlated with differences in locality. Although every part of the skeleton that was studied exhibited these differences, it is evident that these changes do not take

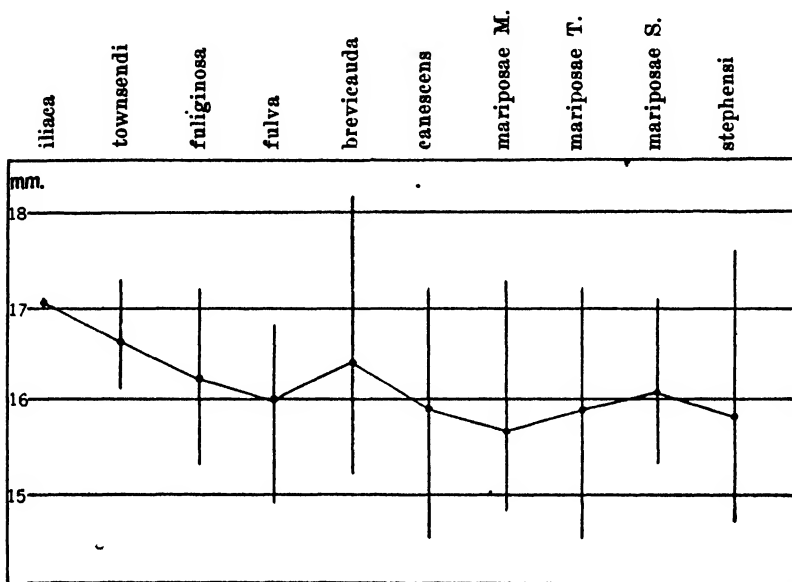


Fig. II. Diagram showing individual and geographic variation in length of furcula for males of ten samples. Length of lines shows range of individual variation; points connected by lines mark positions of averages.

place uniformly throughout the skeleton nor do they correspond to the distance in miles which may separate the localities from which the collections were taken.

The statistical reliability of these deviations is partially indicated in table 22 which is based on a formula used by Frost (1927, formula 6). The purpose of the table is to express by means of a single index number the resemblances between two taxonomic groups of organisms (in this case populations of *Passerella iliaca* from more or less widely separated localities). Any attempt to accomplish such an end is necessarily burdened with many difficulties of major import which tend to detract from the significance of the value assigned to each pair of populations compared. In the beginning, it is acknowledged that such an index number cannot be expected to represent the

true relationship between any two such groups of organisms as are here dealt with. Too many little known factors are concerned with the determination of that relation for us to expect to express it properly through such simple computations as the ones made.

However, the index numbers obtained by the use of this formula give a more concise, more nearly accurate value to the similarities considered than any other means of comparison with which I am familiar. The order of the various similarities between the populations, as indicated by the series of numbers, if arranged in order from zero up corresponds almost exactly with the order of the same similarities if based on concepts acquired through handling and measuring hundreds of skins and skeletons. Even if it is possible for the person who works with the material to sense the relative degrees of likeness between each two populations involved, it is practically impossible to express these concepts intelligently by methods commonly used by taxonomists.

It is not claimed that the values given in table 22 are representative of the genetic relationships between the various pairs of populations, but it is thought that they represent satisfactorily (except where the number of individuals used is too small) the degrees of morphological divergence, in the characters used, in the contrasted populations.

For an explanation of the formulas used in constructing this table see Garrett (1926) and Frost (1927). Each of the values in the main table is the square of a result obtained by a formula (explained in statistical textbooks) for the reliability of the difference in the means of the two groups, indicated on the left in the table, in respect to the character named at the top of the column. For example, in the first line of the first column 151.29 is the result of solving this expression:

$$\frac{M_{xa} - M_{xb}}{\sigma_d}$$

which is the

$$\left| \frac{\begin{array}{c} \text{mean of length of ramus of } \textit{brevicauda} \text{ minus mean of} \\ \text{length of ramus of } \textit{canescens} \end{array}}{\text{standard deviation of the difference}} \right|^2$$

In this particular example the expression with the proper values in place for solving is:

$$\left| \frac{24.56 - 21.98}{\sqrt{\left(\frac{.52}{\sqrt{28}}\right)^2 + \left(\frac{.67}{\sqrt{14}}\right)^2}} \right|^2 = 151.29$$

The figure 417 in the next to the last column of the first line is the sum of all the values in the line and the figure 32 in the last column is that sum divided by the number of characters used (13). When the number in the last column is less than four the probability is great that the two populations compared are practically identical in the characters measured. The value in the first line (32) indicates practical certainty that the differences between the means of the thirteen characters used in *brevicauda* and *canescens* are not due to random sampling. In the next line the obtained value (34) is more reliable

TABLE 21

| Last based on table       | Value | Corrected list            |
|---------------------------|-------|---------------------------|
| brevicauda—mariposae M.   | 34    | brevicauda—mariposae M.   |
| brevicauda—canescens      | 32    | brevicauda—canescens      |
| brevicauda—mariposae T.   | 30    | brevicauda—mariposae T.   |
| mariposae M.—stephensi    | 23    | mariposae M.—stephensi    |
| canescens—mariposae S.    | 17    | canescens—stephensi       |
| mariposae T.—stephensi    | 15    | canescens—mariposae S.    |
| mariposae M.—mariposae S. | 14    | mariposae T.—stephensi    |
| canescens—stephensi       | 13    | mariposae M.—mariposae S. |
| mariposae T.—mariposae S. | 11    | mariposae T.—mariposae S. |
| brevicauda—stephensi      | 5     | brevicauda—stephensi      |
| brevicauda—mariposae S.   | 5     | brevicauda—mariposae S.   |
| canescens—mariposae M.    | 5     | canescens—mariposae M.    |
| canescens—mariposae T.    | 3     | canescens—mariposae T.    |
| mariposae S.—stephensi    | 2     | mariposae S.—stephensi    |
| mariposae M.—mariposae T. | 1     | mariposae M.—mariposae T. |

than that of the first line because a greater number of individuals was used in its computation (more than twenty-five). A close study of the table along with the map (fig. J) showing the geographic positions of the various populations and the tables giving means and numbers of specimens used will demonstrate the value of this method of showing the degree of similarity between groups of *Passerella iliaca*.

It is instructive to arrange, with table 22 as a basis, the various contrasted populations in a list with the most dissimilar pair at the top and the most nearly identical pair at the bottom. Such a list has been made (table 21) and corrected by use of all the information available from other sources. It is remarkable that only one shift from the arrangement of the first list could be made and that this shift was so small.

TABLE 22

STATISTICAL COMPARISONS OF SAMPLES IN RESPECT TO INTERNAL STRUCTURES

|                            | Length<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula | Total  | Average |
|----------------------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|--------|---------|
| brevicauda: canescens      | 151 29          | 9 06              | 32 11            | 83 35            | 76 38           | 31 27           | 67 57            | 46                | 1 28             | 65 29          | 4 80               | 8 64              | 5 29              | 417 00 | 32      |
| brevicauda: mariposae M.   | 116 64          | 15 92             | 89               | 6 00             | 35 28           | 45 97           | 27 77            | 60 68             | 02 46            | 79 50          | 41                 | 2 99              | 24 70             | 434 06 | 34      |
| brevicauda: mariposae T.   | 94 28           | 12 18             | 35 15            | 52 33            | 29 33           | 52 20           | 07 54            | 31                | 23 40            | 45 46          | 38 26              | 42                | 9 18              | 386 18 | 30      |
| brevicauda: mariposae S.   | 1 08            | 11                | 47               | 10 4             | 04              | 81 4            | 32 15            | 52                | 3 42             | 17 72          | 15 52              | 3 02              | 4 04              | 70 17  | 5       |
| brevicauda: stephensi      | 2 50            | 1 39              | 02               | 2 56             | 25              | 2 40            | 20               | 7 24              | 3 46             | 6 50           | 18 15              | 12 89             | 16 08             | 73 64  | 5       |
| canescens: mariposae M.    | 24 01           | 07                | 63 16            | 32 1             | 72              | 04 3            | 13 2             | 28                | 2 02             | 7 51           | 4 41               | 2 46              | 1 72              | 66 32  | 5       |
| canescens: mariposae T.    | 17 06           | 00                | 00               | 78               | 34              | 1 37            | 5 43             | 1 04              | 76               | 2 79           | 2 04               | 2 02              | 00                | 33 63  | 3       |
| canescens: mariposae S.    | 112 36          | 7 02              | 8 18             | 5 29             | 12 53           | 5 02            | 23 14            | 9 42              | 14 36            | 10 69          | 13 03              | 1 54              | 01 22             | 59     | 17      |
| canescens: stephensi       | 16 38           | 2 28              | 1 61             | 1 25             | 20 07           | 17 22           | 60 53            | 10 56             | 12 46            | 17 64          | 9 49               | 24                | 08                | 169 81 | 13      |
| mariposae M.: mariposae T. | 24              | 06                | 89               | 3 17             | 51              | 1 59            | 38               | 30                | 28               | 68             | 51                 | 02                | 2 86              | 11 49  | 1       |
| mariposae M.: mariposae S. | 69 06           | 12 89             | 15 05            | 24 30            | 8 41            | 6 10            | 8 94             | 5 43              | 9 12             | 1 19           | 5 38               | 9 99              | 9 30              | 185 16 | 14      |
| mariposae M.: stephensi    | 125 44          | 3 96              | 3 84             | 14 06            | 16 40           | 22 94           | 28 84            | 61 47             | 7 45             | 5 48           | 2 59               | 4 04              | 1 72              | 298 23 | 23      |
| mariposae T.: mariposae S. | 59 29           | 9 67              | 16 00            | 8 00             | 10 05           | 1 90            | 5 24             | 6 60              | 10 18            | 2 76           | 7 18               | 8 41              | 1 32              | 146 60 | 11      |
| mariposae T.: stephensi    | 106 09          | 2 96              | 1 99             | 3 13             | 17 56           | 14 36           | 19 89            | 7 73              | 8 82             | 7 45           | 4 20               | 4 08              | 09                | 198 35 | 15      |
| mariposae S.: stephensi    | 8 07            | 64                | 94               | 1 10             | 79              | 4 71            | 3 42             | 32                | 05               | 1 30           | 28                 | 60                | 2 04              | 24 26  | 2       |

Figure JJ, in which the mean values for males of seven races and for five characters have been laid off to a scale on vertical lines, shows how nearly the arrangements of the populations agree in different lines of variation. Symbols were used in place of the names of the races or localities so that the order of arrangement might be more easily compared in the five characters. It should be kept in mind that in the two lines on the left the scale ( $\times 20$ ) is just one-half that of the other three lines ( $\times 40$ ). Then, the geographic range in the first two is nearly twice that of the most variable of the other three characters represented. On the other hand, length of sternum and length of humerus exhibit the least range and consequently are considered to be less variable geographically than the other characters.

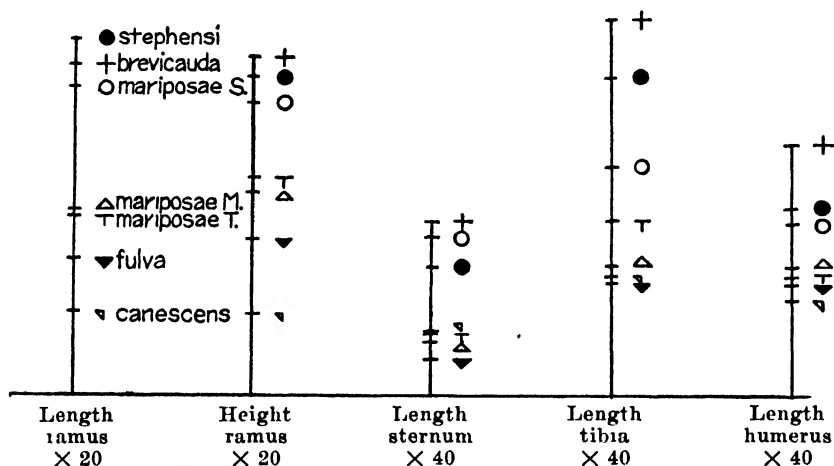


Fig. JJ. Diagram showing arrangement of mean values of seven samples in respect to five characters.

This diagram furnishes further proof that the several populations represented do not vary uniformly. Not one race occupies the same position, with respect to the others, in all the columns. The most extensive changes of relative position are found in *stephensi*, which changes from the top rank in length of ramus to third from the top in length of sternum, and *canescens*, which changes from lowest position in length of ramus, height of ramus, and length of humerus to fourth from the lowest in length of sternum.

Another point to be kept in mind in examining this diagram is that the means plotted are not necessarily those of the extreme races within the species but that they are limited to those samples of the schistacea group which were sufficiently large for the means to be fairly reliable.

TABLE 23  
COMPARISON OF MEAN VALUES OF EACH CHARACTER IN EACH SAMPLE WITH THOSE OF MALES OF *iliaca*

| Sample                    | Sex | Width<br>hacri-<br>mal | Width<br>skull | Length<br>ramus | Height<br>ramus | Length<br>sternum,<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula |
|---------------------------|-----|------------------------|----------------|-----------------|-----------------|-------------------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|
| <i>iliaca</i> .....       | ♂   | 100                    | 100            | 100             | 100             | 100                           | 100              | 100              | 100             | 100             | 100              | 100               | 100              | 100            | 100                | 100               | 100               |
| <i>iliaca</i> .....       | ♀   | 97                     | 100            | 97              | 96              | 91                            | 99               | 93               | 99              | 95              | 99               | 102               | 96               | 97             | 98                 | 95                | 101               |
| <i>townsendi</i> .....    | ♂   | 97                     | 103            | 102             | 98              | 85                            | 100              | 99               | 105             | 102             | 103              | 98                | 94               | 95             | 96                 | 98                | 98                |
| <i>townsendi</i> .....    | ♀   | 95                     | 101            | 99              | 95              | 82                            | 95               | 98               | 103             | 101             | 103              | 94                | 90               | 91             | 92                 | 93                | 96                |
| <i>fuliginosa</i> .....   | ♂   | 96                     | 102            | 101             | 96              | 84                            | 97               | 98               | 104             | 102             | 103              | 96                | 92               | 93             | 95                 | 96                | 95                |
| <i>fuliginosa</i> .....   | ♀   | 96                     | 100            | 98              | 93              | 80                            | 95               | 96               | 100             | 100             | 100              | 92                | 88               | 89             | 89                 | 91                | 93                |
| <i>fulva</i> .....        | ♂   | 99                     | 104            | 99              | 124             | 82                            | 91               | 90               | 99              | 93              | 98               | 94                | 92               | 93             | 92                 | 94                | 94                |
| <i>fulva</i> .....        | ♀   | 94                     | 102            | 96              | 117             | 77                            | 89               | 92               | 95              | 91              | 95               | 89                | 87               | 88             | 87                 | 89                | 90                |
| <i>brevicauda</i> .....   | ♂   | 110                    | 113            | 108             | 156             | 84                            | 93               | 94               | 103             | 100             | 102              | 98                | 96               | 97             | 97                 | 98                | 96                |
| <i>brevicauda</i> .....   | ♀   | 105                    | 110            | 108             | 150             | 80                            | 90               | 91               | 100             | 98              | 100              | 94                | 91               | 92             | 92                 | 95                | 94                |
| <i>canescens</i> .....    | ♂   | 98                     | 101            | 97              | 111             | 85                            | 92               | 91               | 99              | 97              | 98               | 94                | 92               | 93             | 91                 | 96                | 93                |
| <i>canescens</i> .....    | ♀   | 91                     | 98             | 93              | 103             | 76                            | 88               | 89               | 96              | 95              | 95               | 91                | 88               | 88             | 87                 | 90                | 90                |
| <i>mariposae M.</i> ..... | ♂   | 101                    | 108            | 101             | 132             | 82                            | 91               | 88               | 99              | 97              | 99               | 94                | 93               | 94             | 93                 | 95                | 92                |
| <i>mariposae M.</i> ..... | ♀   | 99                     | 105            | 100             | 131             | 79                            | 88               | 88               | 97              | 96              | 97               | 91                | 88               | 90             | 90                 | 91                | 90                |
| <i>mariposae T.</i> ..... | ♂   | 101                    | 106            | 101             | 135             | 82                            | 92               | 90               | 99              | 97              | 99               | 94                | 93               | 94             | 92                 | 95                | 93                |
| <i>mariposae T.</i> ..... | ♀   | 98                     | 105            | 99              | 130             | 78                            | 90               | 90               | 98              | 96              | 98               | 91                | 88               | 90             | 89                 | 90                | 91                |
| <i>mariposae S.</i> ..... | ♂   | 108                    | 111            | 107             | 148             | 84                            | 95               | 93               | 101             | 98              | 100              | 96                | 94               | 95             | 94                 | 97                | 94                |
| <i>mariposae S.</i> ..... | ♀   | 103                    | 108            | 106             | 140             | 79                            | 92               | 90               | 99              | 96              | 99               | 93                | 89               | 91             | 90                 | 93                | 93                |
| <i>stephensi</i> .....    | ♂   | 110                    | 112            | 110             | 153             | 83                            | 93               | 92               | 102             | 100             | 102              | 96                | 95               | 96             | 94                 | 96                | 93                |
| <i>stephensi</i> .....    | ♀   | 105                    | 110            | 109             | 152             | 79                            | 92               | 89               | 100             | 97              | 100              | 92                | 89               | 91             | 89                 | 93                | 93                |
| <i>Range</i> .....        |     | 17                     | 15             | 17              | 63              | 24                            | 12               | 12               | 9               | 11              | 8                | 13                | 13               | 12             | 13                 | 11                | 11                |

Two means of presentation have been used for showing the nature of the differences in proportions of skeletal parts in different populations. First, the mean values for each character measured have been compared with the mean value for that particular character in the

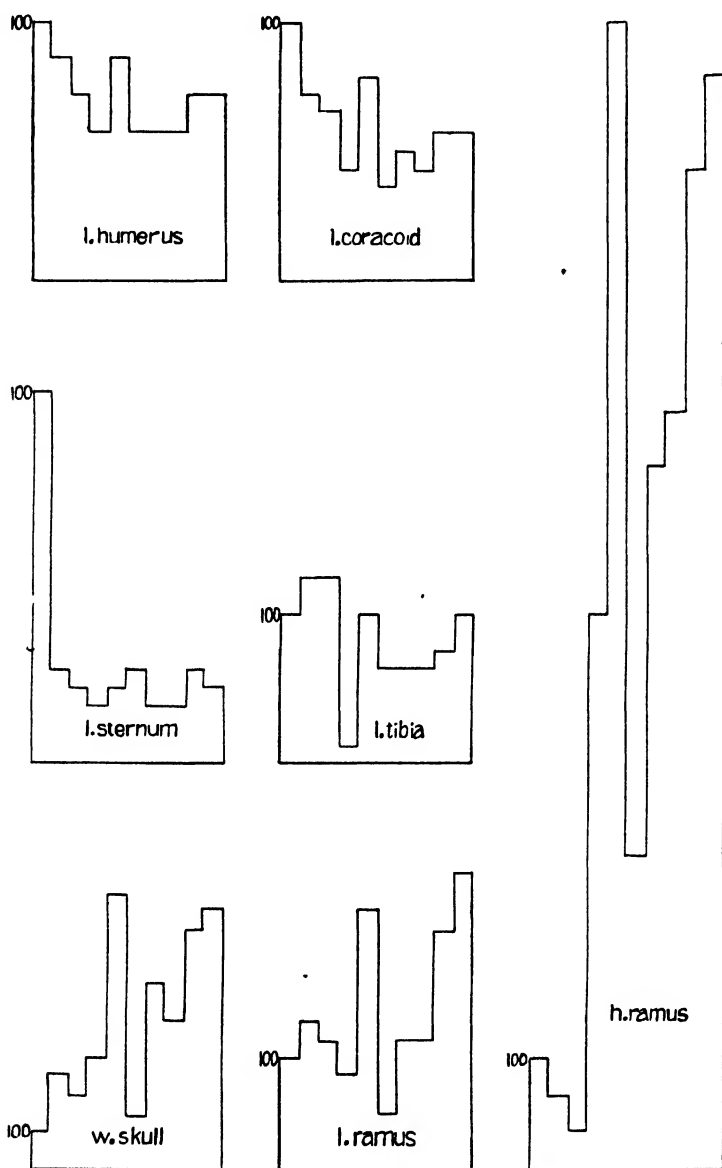


Fig. KK. Column diagrams showing comparisons of mean values with those of *ilua* in seven characters.

See table 23 and text.

TABLE 24

COMPARISON OF MEAN VALUES OF EACH CHARACTER IN EACH SAMPLE WITH THOSE OF LENGTH OF TIBIA

| Sample       | Sex | Width<br>lacrimal | Width<br>skull | Length<br>ramus | Height<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>for ulna |
|--------------|-----|-------------------|----------------|-----------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|--------------------|
| iliaca       | ♂   | 25                | 51             | 64              | 17              | 77                | 29               | 43               | 58              | 100             | 69               | 60                | 62               | 69             | 54                 | 64                | 48                 |
| iliaca       | ♀   | 25                | 51             | 63              | 17              | 71                | 29               | 41               | 59              | 100             | 70               | 62                | 61               | 68             | 53                 | 62                | 49                 |
| townsendi    | ♂   | 24                | 51             | 64              | 17              | 64                | 28               | 42               | 59              | 100             | 70               | 57                | 57               | 64             | 50                 | 61                | 46                 |
| townsendi    | ♀   | 24                | 50             | 63              | 16              | 62                | 27               | 42               | 59              | 100             | 70               | 56                | 55               | 62             | 48                 | 59                | 46                 |
| fuliginosa   | ♂   | 24                | 50             | 63              | 15              | 63                | 27               | 42               | 59              | 100             | 70               | 56                | 56               | 63             | 48                 | 60                | 44                 |
| fuliginosa   | ♀   | 24                | 50             | 63              | 16              | 61                | 27               | 42               | 58              | 100             | 70               | 56                | 55               | 62             | 48                 | 59                | 45                 |
| fulva        | ♂   | 26                | 55             | 66              | 22              | 65                | 27               | 40               | 60              | 100             | 70               | 59                | 59               | 67             | 51                 | 62                | 47                 |
| fulva        | ♀   | 26                | 55             | 66              | 22              | 63                | 27               | 42               | 59              | 100             | 70               | 57                | 57               | 65             | 50                 | 61                | 46                 |
| brevicauda   | ♂   | 28                | 57             | 69              | 27              | 64                | 26               | 40               | 59              | 100             | 70               | 59                | 59               | 67             | 51                 | 62                | 46                 |
| brevicauda   | ♀   | 27                | 56             | 70              | 27              | 63                | 26               | 40               | 60              | 100             | 70               | 58                | 57               | 65             | 50                 | 62                | 46                 |
| canescens    | ♂   | 26                | 53             | 64              | 20              | 65                | 27               | 41               | 60              | 100             | 69               | 58                | 59               | 67             | 51                 | 64                | 47                 |
| canescens    | ♀   | 24                | 52             | 63              | 19              | 62                | 27               | 41               | 59              | 100             | 71               | 59                | 59               | 68             | 51                 | 63                | 46                 |
| mariposae M. | ♂   | 27                | 56             | 67              | 24              | 65                | 27               | 40               | 60              | 100             | 70               | 57                | 57               | 64             | 50                 | 60                | 44                 |
| mariposae M. | ♀   | 26                | 55             | 66              | 24              | 62                | 26               | 39               | 59              | 100             | 70               | 58                | 59               | 67             | 51                 | 62                | 46                 |
| mariposae T. | ♂   | 26                | 58             | 66              | 24              | 66                | 27               | 40               | 60              | 100             | 71               | 58                | 57               | 65             | 50                 | 61                | 46                 |
| mariposae T. | ♀   | 26                | 56             | 67              | 24              | 63                | 27               | 41               | 60              | 100             | 71               | 59                | 60               | 67             | 51                 | 63                | 46                 |
| mariposae S. | ♂   | 28                | 57             | 70              | 26              | 66                | 27               | 41               | 60              | 100             | 71               | 58                | 57               | 65             | 50                 | 62                | 45                 |
| mariposae S. | ♀   | 27                | 57             | 70              | 25              | 63                | 27               | 40               | 60              | 100             | 71               | 58                | 59               | 66             | 50                 | 62                | 46                 |
| stephensi    | ♂   | 28                | 57             | 72              | 27              | 65                | 27               | 40               | 60              | 100             | 71               | 58                | 57               | 66             | 49                 | 62                | 46                 |
| stephensi    | ♀   | 28                | 57             | 72              | 27              | 63                | 27               | 40               | 60              | 100             | 71               | 58                | 57               | 65             | 49                 | 62                | 46                 |
| Range        |     | 4                 | 8              | 9               | 12              | 16                | 3                | 4                | 2               | 0               | 2                | 6                 | 7                | 7              | 6                  | 5                 | 5                  |



series of male *iliaca*. The mean for *iliaca* (males) was called 100 per cent and the proper value computed for each of the other samples by dividing their means by that of *iliaca* for that character. Table 23 gives these ratio values for the sixteen characters measured in both sexes of samples of ten populations.

The column diagrams in figure KK show in a more graphic way the ratios of the mean values for males in a few of the characters. Each column represents the ratio of one sample, the first on the left being *iliaca*—the others arranged in the same order as in table 23.

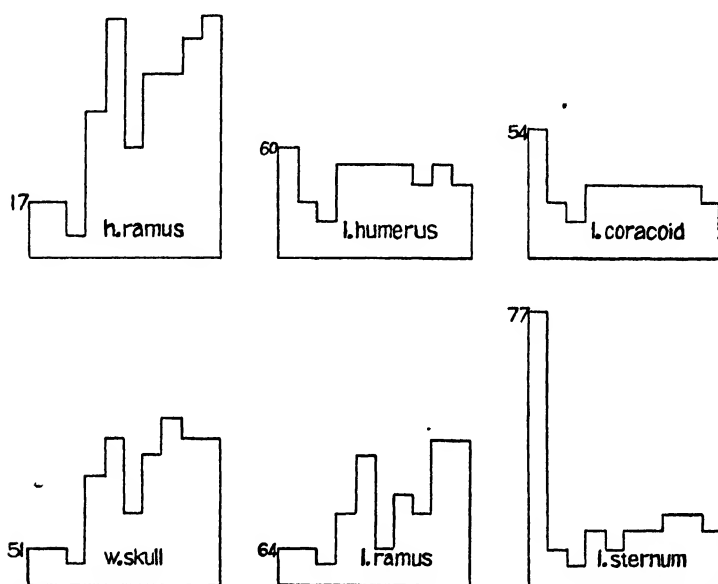


Fig. LL. Column diagrams showing comparisons of mean values with those of length of tibia in six characters.

See table 24 and text.

Table 24 was prepared in the same way as table 23 except that the tibia length, in each sample, was given the value of 100 per cent and all the means of other characters in that sample were compared with it. Length of tibia was used as 100 per cent because it represented the longest measurement and because this bone is one of the less variable, individually, in the skeleton. This table gives an approximation of the geographic correlation between the various characters. Those characters which exhibit the least range, in per cent, between the samples are the most closely correlated geographically with length of tibia. In the column diagrams in figure LL the samples are represented in the same order as in figure KK. The number at the top of the first column in each diagram represents the ratio of the mean of

*iliaca*, in the character concerned, to the mean of length of tibia in the same sample population. If the various races of fox sparrows varied uniformly in all the characters, the columns in each diagram would all be of the same height.

No measurements of external characters were made on the specimens that were used in this study so that the exact amount of correlation between external and internal characters could not be determined. The table of measurements of the subspecies of *Passerella iliaca* given by Swarth (1920, pp. 182, 183) was used as a basis for comparison with measurements of skeletal characters. It must be kept in mind that Swarth's table represents small samples (ten or fewer specimens) and that the localities represented in it are not the same as for the material used in the present work. It is, therefore, necessary to be content in this account merely to call attention to those instances in which there is an evident correlation between internal and external features of structure.

The various degrees of development of the horny sheath of the bill, exhibited by the races of fox sparrows, are all reflected not only in a like degree of development of the bones of the bill, as might be expected, but are paralleled also in the other parts of the skull. In those populations which are characterized by having exceptionally massive bills practically every bone in the skull is massive and heavy. Apparently even such portions of the skull as little subject to muscular stress as the interorbital septum, share in this excess bony development. It is not intended to imply that this general massiveness constitutes all the geographic variation in the skull, for some variation in proportion between measurements of the skull has already been mentioned. However, this general massiveness is the most conspicuous of the several variable features found in the skull.

It is of interest to note that the subspecies (*iliaca*) which has the longest sternum also has the longest wing (flight feathers) measurement and that each of the other subspecies bears nearly the same relation to *iliaca* in respect to both these characters. There appears to be a still greater correlation between length of wing and length of the wing bones (humerus, radius, and ulna). The closeness of the ratios obtained in a comparison of the subspecies with *iliaca*, in respect to these internal measurements and to wing length, indicates a surer basis than mere chance.

Length of tarsus is so nearly the same measurement externally as internally that measurements of these characters in one series of specimens should be exactly parallel, provided that the measurements

are made uniformly. There is little doubt that there is less error in measuring the length of the bone than in making the external measurement of tarsal length, especially when these measurements are made by different persons or at different times.

A careful comparison of the tables of average measurements revealed one other instance of characters used in this study being paralleled in degree of development by characteristics usually measured externally. There is a noticeable geographic fluctuation in the amount of development of the toes which appears to be correlated with the extent of development of the larger bones of the bird's leg.

#### ADAPTIVE SIGNIFICANCE, WITH REFERENCE TO THE ENVIRONMENT

Several structural features of *Passerella iliaca* are of such a nature as to justify a consideration here of their adaptive significance, with reference to environment. The remarkable development of the bill in some of the fox sparrows, when contrasted with the comparatively weaker development in some other divisions of the species might suggest that each of these various degrees of development has some particular adaptational value for the birds which possess it. Two considerations of this problem, in groups of birds comparable with fox sparrows, have been mentioned earlier in this paper and the fact pointed out that the authors' conclusions were not in agreement.

In a consideration of the significance of the varying degrees of bill development in the fox sparrow three lines of evidence may be presented as aids in interpretation. First, this characteristic follows a rather even gradient, reaching the extreme in greatness at the ends of two separated lines of development. This implies, if birds with large bills have some special need for them, that a similar necessity has arisen and has been fulfilled in two widely separated localities. Then, as has been mentioned, in those birds which have large bills there is a tendency for bones in other parts of the skeleton to be heavier and larger. Finally, the most pertinent evidence bearing on this question is that obtained from a consideration of the food habits of the species. It is assumed that if enlarged bills have some special value that value lies in their making accessible some special kind of food such as hard-shelled or large seeds which birds with small bills cannot eat. It is further supposed that this differentiation must have taken place in the summer habitat of the birds since the summer is the only time of year that the birds are segregated with respect to this character. Field observation of the feeding habits of five races, among

which are some showing extremes of bill development in both directions, and a detailed examination of the stomach contents of ten individuals killed in summer (see p. 283) indicate pretty conclusively that the food of this species in summer is uniformly almost entirely composed not of seeds but of animal matter which is soft.

All the fox sparrows have large, well developed feet and all of them have the habit of scratching developed to a high degree. Here then is a structure which is highly developed and which is certainly of direct benefit to the birds because of that special development. It has been pointed out that there is a slight difference in the degree of development of this feature of structure (see p. 360) and it would seem likely that such differential development might have some significance with respect to the efficiency of the scratching habit, but there are no facts known to the writer which prove the truth of such an inference.

While the subject of adaptation is being considered it may be well to present some facts bearing on the question of coloration, even though this is not a skeletal characteristic. It is desirable at this point to call attention to Swarth's (1920, p. 90) explanation of the varying degrees of intensity of coloration in the *unalaschensis* group of subspecies in which he suggests that the differences in color may be due to varying degrees of humidity experienced by the birds throughout the year rather than during the breeding season alone.

Within the *schistacea* group of fox sparrows gray is the predominating color and there is not a great amount of variation. In the course of field work on the north side of Mount Lassen, in the summer of 1926, it was noted by the present writer that whenever birds were shot so that they fell to the ground with their backs showing they were so well concealed as to be almost invisible against the background of volcanic ash which matched them so closely in color. This resemblance in color of the backs of the birds to the soil over which they lived was also noted in other California races. It was especially noticeable in the Yolla Bolly Mountains race where there is a distinct tendency for the birds to be brownish and where the soils are, in general, darker than within the ranges of the other races. Here then, is a case in which a trend of variation in fox sparrows may be correlated with an environmental factor.

In all parts of the range of the species fox sparrows migrate, and as has been indicated by Swarth (1920, p. 105) it may in general be said that the subspecies breeding farthest north migrate farthest south. Thus, there is a great variation in length of migration route

within the species. Birds of the subspecies *iliaca* have a much longer migration route than those of any other group. The amount by which this race is set off from the others in respect to length of migration is roughly paralleled in proportion by the amount that it is set off from the others in respect to length of sternum and to a lesser extent, length of those bones (humerus, radius, ulna, coracoid, scapula, and furcula) which appear to be closely correlated with the sternum in length. A similar behavior of these characters when compared with length of migration route may be noted in the case of other subspecies, but in none is it so prominent as in *iliaca*. Every part of the skeleton used considerably in flight has been developed to a high degree as an accompaniment to a lengthened line of migration flight.

Diverse attempts have been made to interpret the existence of features of structure by which species are distinguished. One of these views is exemplified by the statement of Grinnell (1926, p. 260) who writes that he has "confidence that not only this [coloration in a race of pocket gopher], but each and every other character which we find to distinguish races, has its full adaptive justification in the scheme of existence."

Conversely, there is the idea set forth by Morgan (1923, p. 24) that a single change in the genetic constitution of an animal often affects different organs and that the end result may be, at the same time, a change in some physiological process and a change in some superficial part of the body. That author further points out that even slight changes in the physiological makeup of a species might importantly affect its chances for survival. It would naturally follow that those superficial characters, whether useful to the animal possessing them or not, which are dependent for their existence upon their relation to some beneficial physiological condition will survive so long as the physiological condition survives.

However, this does not imply that some features of external structure could not be preserved because of some survival value which they themselves possess. If the first of these two views is modified by interpreting "adaptive justification" so that it includes those examples in which superficial characters are preserved merely by reason of their being linked with some beneficial physiological characteristic, it would seem reasonable to say that the preservation of these superficial characters may be due either to a direct benefit to the species or to their correlation with some beneficial physiological character. Skeletal characters, for purposes of this consideration, may be placed in the same class as the superficial characters.

## COMPARISON OF PASSERELLA WITH MELOSPIZA

Further evidence bearing on the relation between the hitherto recognized genera *Passerella* and *Melospiza* will be presented at this point. The summary of an analysis of Ridgway's (1901) characterizations of these genera is presented in the accompanying tabulation. Practically all the characters which are contrasted in the two diag-

TABLE 25

TABULATION OF CHARACTERS ASSIGNED TO *Melospiza* AND *Passerella* BY  
RIDGWAY (1901)

| Melospiza   | Passerella  |
|---|---|
| Medium sized, rather small, or large.   | Medium sized.   |
| Wing $2\frac{2}{3}$ to barely more than 3 as long as tarsus.  | Wing $3\frac{1}{2}$ to $3\frac{2}{3}$ as long as tarsus.  |
| 8th to 5th primaries longest.   | 8th to 6th primaries longest.   |
| Gonys straight or faintly convex.   | Gonys straight or faintly convex.   |
| Tarsus about equal to middle toe with claw.   | Middle toe with claw about equal to tarsus.   |
| Tail equal to or slightly longer than wing, decidedly shorter than wing, or intermediate, less than half overlaid by upper coverts. | Tail $\frac{5}{6}$ as long as wing to longer than wing, about half concealed by upper coverts.  |
| Scutella [of tarsus] fairly distinct.   | Scutella [of tarsus] fairly distinct.   |
| Lateral claws not reaching to base of middle claw.  | Lateral claws reaching decidedly past base of middle claw.                                      |
| Hallux about equal to inner toe, its claw nearly as long as the digit.  | Hallux about equal to middle toe or a little shorter, its claw about equal to digit or shorter. |
| Primaries exceeding secondaries by much less than length of tarsus.   | Primaries exceeding secondaries by less than length of tarsus.                                  |
| Mandibular tomium straight to sub-basal angle.  | Mandibular tomium straight to sub-basal angle.  |
| Exposed culmen never much more than half as long as tarsus.   | Tarsus rather long (about twice as long as exposed culmen).                                     |

noses are here compared. Inspection of the tabulation reveals that in all except two of the characters the two groups are essentially identical. In respect to length of wing compared with length of tarsus there is a definite hiatus between the two, according to Ridgway. The measurements given by Ridgway, however, show little actual difference in this character between some races of the two groups.

His average measurements of ten males of *Passerella iliaca townsendi* show the wing to be a little less than 3.2 times as long as the tarsus. The wing is 3.1 times as long as the tarsus in his averages of forty-one males of *Melospiza m. melodia*. According to Swarth's measurements of ten males of *P. i. townsendi* the wing is 3.1 times as long as the tarsus. It is evident, then, that the more migratory song sparrows have wings as long, relative to tarsal length, as the more sedentary of the fox sparrows.

Ridgway's diagnoses of these two groups indicate that they may be separated on the basis of length of outer toe and claw relative to the length of middle toe and claw. While it is possible to measure these characters it seems doubtful whether it is practicable to rely upon these measurements in making comparisons; in fact, it seems that to present these measurements would be misleading in this case. All the skins of both groups in the Museum of Vertebrate Zoology were examined with a view to determining the status of this character, with the following results: In some races of song sparrow the outer claw does not reach so far as the base of the middle claw; in others it reaches decidedly past the base of the middle claw. In some races of fox sparrow the outer claw persistently reaches past the middle of the middle claw; in others it does *not* reach so far as the middle of the middle claw. There is a definite hiatus between the two groups in this character, but in each of the two groups geographic variation, and to some extent individual variation, is as great as or greater than the difference between the two.

In order to make a further comparison skulls of seven races of each of these two groups were selected at random. These were then arranged by first picking out the one with the most massive palatine bones, then placing beside it the one most similar to it. This procedure was continued until a series was completed in which each two adjacent skulls appeared, upon gross examination, to be more nearly alike than any other two (see pl. 20). Although the two extremes in this series of skulls are remarkably unlike, the gradation between them is so even that it is difficult to separate the series into two groups. In this series the first seven skulls were all in the species *iliaca* which indicated that the two groups did not overlap in respect to skull characters discernible to the eye. However, the interval separating them was smaller than was evident between several of the other pairs of adjacent skulls.

Several tendencies to vary may be traced gradually from one extreme of the series to the other. At one extreme is a massive skull, wide in proportion to length, with prominent, enlarged auditory bullae, with large and much divided palatine bones, and with a well developed interorbital septum. All these characters change gradually through the series to the opposite extreme which is light and narrow in proportion to length, with inconspicuous, small auditory bullae, with

TABLE 26

MEASUREMENTS, AND RATIOS BETWEEN THEM, OF FOX SPARROW AND SONG SPARROW SKULLS

| Race          | Width, lacrimal | Width, skull | Length, skull | Width, lacrimal | Width, skull    |
|---------------|-----------------|--------------|---------------|-----------------|-----------------|
|               |                 |              |               | Width, skull    | Length, skull   |
|               |                 |              |               | <i>per cent</i> | <i>per cent</i> |
| stephensi     | 10 2            | 21 0         | 34 7          | 49              | 60              |
| brevicauda    | 9 8             | 20 8         | 34 5          | 47              | 60              |
| unalaschensis | 9 0             | 17 9         | 32 2          | 50              | 56              |
| sinuosa       | 8 2             | 18 4         | 31 8          | 45              | 57              |
| iliaca        | 8 6             | 18 2         | 31 4          | 47              | 58              |
| fuliginosa    | 7 4             | 17 2         | 31 8          | 43              | 54              |
| schistacea    | 7 7             | 16 5         | 30 2          | 47              | 54              |
| fisherella    | 7 1             | 15 9         | 31 0          | 45              | 51              |
| melodia       | 7 3             | 15 8         | 28 2          | 46              | 56              |
| pusillula     | 6 6             | 15 0         | 28 0          | 44              | 54              |
| l. lincolni   | 6 6             | 14 7         | 28 8          | 45              | 51              |
| mailliardi    | 6 9             | 15 0         | 30 5          | 46              | 49              |
| rufina        | 6 7             | 14 7         | 30 2          | 46              | 49              |
| sanaka        | 8 6             | 17 2         | 36 7          | 50              | 47              |

NOTE The first seven races belong to the fox sparrow group, the second seven to the song sparrow group

small and little divided palatine bones, and with slightly developed interorbital septum. However, in respect to size (length) the smallest skull is not at one end of the series but is near the center of the line, while the two end skulls are longest and second longest respectively. Table 26 shows the order of arrangement of the races in the series of skulls just described and gives measurements of width of skull at lacrimal, greatest width and length of skull with ratios between the first and second of these and between the second and third.



## CONCLUSIONS

Young birds of the species *Passerella iliaca* gain the proportions of adults soon after leaving the nest and thereafter there is very slight, if any, change in the size of the bones due to age. In respect to sex, there is a definite though small difference in size, the males being slightly larger than the females. Individual variation in size of most parts of the skeleton is slight when compared with geographic variation.

The amount of variation computed for each skeletal characteristic does not differ materially, except in being more accurately determined, from the amount of variation of closely correlated external features of structure as determined from smaller samples. The direction of variation of internal structure parallels closely the direction of variation as determined from the study of external structure. This analysis has shown that in some cases the manner of change between populations designated by subspecific rank differs in some respects from that ascribed to it as a result of the usual method of comparing study skins. These results indicate that a more gradual change exists, for example, between the subspecies *mariposae* and *stephensi* than has heretofore been ascribed to them.

Several of the observed trends of variation may be considered with a view to discovering some hints as to whether or not they have some adaptive significance with reference to the environment. In the face of all the evidence now available it seems impracticable to attempt to assign some value, for the individuals possessing them, to any of the various degrees of development of the skull and bill in the races of fox sparrow. It is not improbable, however, that these various degrees of development may be closely correlated with some other feature of structure or with some type of physiological reaction which has some particularly marked value to the species in some parts of its range.

It is much more easily conceived that those various degrees of development of the structures connected with flight have an intimate relation to the use of flight powers in migration. In every case the samples with large bones in the wings and pectoral girdle belong to races which have long migration routes and the samples with those bones weakly developed belong to relatively sedentary races.

A consideration of all the available means for comparison between the groups *Passerella* and *Melospiza* reveals that they are so closely related as to, in my opinion, belong in the same genus. Since *Passerella* is the older name it is proposed that *Melospiza* Baird (1858) be merged with *Passerella* Swainson (1837). The following lines of evidence are reviewed in support of this conclusion:

1. The two genera were established without their authors having sufficient material to determine properly the relation existing between them. Baird (author of *Melospiza*) prefaced his treatment of the Fringillidae with the statement that he did not claim that his arrangement showed the true relationships between genera.

2. Although the close relation between these two groups has been pointed out often I am not aware that anyone has previously attempted, with adequate material, a thorough investigation of that relation.

3. No constant differences in external structure, of generic value, could be found in the diagnoses of the genera except with respect to length of outer toe compared with middle toe and that character is highly variable in both groups; in fact the range in each group is equal to, or greater than, the hiatus between them.

4. There is no constant difference in coloration; even the possession of the characteristic grouping of spots in the center of the breast is common to both groups.

5. The distribution of the two groups indicates an intimate relationship, as Swarth has shown.

6. The two groups have many common features as regards migratory habit although the song sparrows tend to be more sedentary than the fox sparrows.

7. In respect to habits there is:

- a. A close similarity in habitat choice, closely related races in both preferring stream sides.
- b. So close a similarity in songs that it is difficult to distinguish between some races.
- c. A close similarity in type of nest and choice of nest site.
- d. A similarity in eggs so close that they are nearly indistinguishable.

8. There is an almost complete intergradation in all the characteristics examined in the structure of the skull. The hiatus between the two groups in each character is almost insignificant when compared with the extent of range of that character in either group.

9. The extraordinarily great geographic variation exhibited by each of these groups is a characteristic which markedly separates them from any adjacent group of sparrows. This characteristic, when the slight differences in structure between them are kept in mind, seems to be conclusive evidence of their close relationship. In the case of such variable birds as these it would seem that differences between genera should be greater, in absolute value, than would be necessary to separate groups which do not vary to such an extent. In most characteristics, however, no hiatus could be discovered between fox sparrows and song sparrows and where one did exist it proved to be surprisingly small.

### GENERAL SUMMARY

An analysis of variation is a prerequisite for studies concerning the systematics, evolution, or paleontology of birds. Many authors have commented on the need for such analysis but few attempts have been made to carry out these suggestions.

*Passerella iliaca* was selected as a fit subject for extensive studies of variation because (1) this species was well known from the study of external features, (2) a great amount of geographic variation in external characters contrasted with slight variation of other sorts, (3) material could be obtained in quantity, and (4) the restricted habitat of the bird gave promise of opportunities to correlate skeletal variation with fluctuations in the environment.

The genus *Passerella* was established by Swainson in 1837. The latest systematic revision of the group shows that it contains one species with sixteen recognized subspecies. All these occur in North America.

A consideration of the available material bearing on the natural history of the fox sparrow shows several well marked tendencies to vary geographically in habits and in responses to the environment. These tendencies to vary follow a definite order and parallels may be pointed out between them and tendencies to vary in features of structure.

Four hundred and sixty-five skeletons of this species have been available for this study. These included representatives of fourteen of the sixteen recognized subspecies.

Characters used in this analysis of variation are: Body-weight, length of skull, width of skull at lacrimal, greatest width of skull, length of ramus, height of ramus, length of sternum, width of sternum, lengths of pelvis, femur, tibia, tarsus, humerus, radius, ulna, coracoid, scapula, and furcula.

A formula was used which successfully compares the resemblances between contrasted groups (in this case samples representing subspecies) with respect to several characters and expresses, in a single number, the degree of similarity in each pair. When based on this formula the order of arrangement of the contrasted pairs of populations could be modified scarcely at all when all other available lines of evidence were used. ‘

Significant geographic variation was found in every part of the skeleton that was examined. The various geographic populations do not vary uniformly with respect to all features of internal structure. Some characters, however, are evidently closely correlated geographically with other characters of internal structure.

The available evidence does not show that the possession of enlarged bill and skull found in some races is of any particular advantage for the birds possessing them. There is some evidence which indicates that some other skeletal features, for example, lengthened sternum, have a distinct value for the birds possessing them.

Evidence of every sort pertaining to the question bears out the conclusion that song sparrows and fox sparrows are so closely related as to belong in the same genus and it is proposed to merge *Melospiza* with *Passerella*.

TABLE 27  
SKELETAL MEASUREMENTS (IN MILLIMETERS) OF MALES OF *Fulca*

| Num-<br>ber | Width<br>lacrmal | Width<br>skull | Length<br>ramus | Height<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula |
|-------------|------------------|----------------|-----------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|
| 48831       | 8 7              | 18 8           | 22 7            | 7 7             | 21 9              | 9 0              | 14 2             | 20 0            | 32 9            | 22 9             | 19 4              | 19 6             | 21 9           | 17 4               | 21 2              | 16 1              |
| 48848       | 9 4              | 18 3           | 22 4            | 7 3             | 22 3              | 9 2              | 13 6             | 20 4            | 32 9            | 23 5             | 20 2              | 19 8             | 22 6           | 17 3               | 21 3              | 15 6              |
| 48834       | 8 5              | 18 8           | 22 6            | 7 7             | 22 1              | 9 3              |                  | 20 1            | 32 9            | 23 8             | 19 9              | 19 9             | 22 5           | 17 5               | 21 3              | 16 3              |
| 48854       | 8 3              | 17 7           | 20 6            |                 | 21 8              | 9 0              | 14 1             | 20 1            | 33 2            | 24 0             | 19 8              | 19 9             | 22 5           | 16 7               | 21 2              | 15 3              |
| 48836       |                  | 18 7           | 22 6            | 7 6             | 22 4              | 9 2              | 14 3             |                 | 33 6            | 23 6             | 19 8              | 20 3             | 22 9           | 17 3               | 21 2              | 15 5              |
| 48830       | 9 0              | 18 5           | 23 3            | 7 4             | 22 4              |                  | 13 1             | 19 5            | 33 7            | 24 3             | 19 4              | 19 9             | 22 5           | 16 8               | 19 9              | 14 9              |
| 48849       | 8 8              | 18 2           | 21 9            | 7 8             | 21 1              | 8 3              | 14 4             | 20 3            | 33 8            | 23 3             | 19 4              | 19 9             | 22 6           | 17 0               | 20 8              | 16 1              |
| 48828       | 8 9              | 18 0           | 21 7            |                 | 23 0              | 9 3              | 12 7             | 20 3            | 33 9            | 23 2             | 20 4              | 20 8             | 23 4           | 17 6               | 22 3              | 16 2              |
| 48825       | 8 5              |                |                 |                 | 22 6              | 9 3              | 14 2             | 20 4            | 34 0            | 24 5             | 19 7              | 19 7             | 22 3           | 17 2               | 20 9              | 16 4              |
| 48853       | 9 0              | 19 2           | 22 1            | 7 7             | 21 8              | 8 5              | 13 8             | 20 2            | 34 1            | 24 0             | 19 8              | 19 9             | 22 3           | 17 7               | 20 0              | 16 0              |
| 48843       | 8 8              | 18 9           | 22 8            | 7 4             | 22 1              | 9 4              | 14 4             | 20 8            | 34 5            | 24 6             | 20 4              | 20 0             | 22 5           | 17 5               | 21 5              | 16 3              |
| 48837       | 9 9              | 19 1           | 22 7            | 7 9             | 23 0              | 9 4              | 14 2             | 20 3            | 34 7            | 23 9             | 20 2              | 20 7             | 23 2           | 17 7               | 21 9              | 15 7              |
| 48846       | 9 1              | 18 5           |                 |                 |                   |                  | 13 4             | 20 5            | 34 7            | 24 2             | 20 6              | 21 1             | 23 4           |                    | 21 7              | 16 8              |
| 48832       | 9 3              | 19 5           | 22 8            | 8 0             | 22 2              | 9 5              | 12 7             | 20 4            | 34 9            | 24 9             | 20 5              | 20 4             | 23 0           | 17 7               | 21 7              | 16 1              |
| 48850       | 8 9              | 18 7           | 22 8            | 7 8             | 22 8              | 10 1             | 13 9             | 20 5            | 35 0            | 24 6             | 20 1              | 20 4             | 23 1           | 17 4               | 21 9              | 16 3              |
| 48829       |                  |                | 22 6            | 7 5             | 22 0              | 9 2              | 14 0             | 20 2            | 35 3            | 24 6             | 21 1              | 20 8             | 23 4           | 17 2               | 21 8              | 16 8              |

TABLE 28  
SKELETAL MEASUREMENTS (IN MILLIMETERS) OF MALES OF *canescens*

| Num-<br>ber | Width<br>lacrimal | Width<br>skull | Length<br>ramus | Height<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula |
|-------------|-------------------|----------------|-----------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|
| 51159       | 8.5               | 17.8           | 21.6            | 6.3             | 21.8              | 9.0              | 14.2             | 19.4            | 32.7            | 23.0             | 19.4              | 19.2             | 21.9           | 16.3               | 20.4              | 15.4              |
| 51158       | 8.1               | 17.7           | 21.1            | 6.5             | 21.8              | 9.3              | 13.6             | 20.0            | 32.9            | 22.9             | 19.7              | 19.9             | 22.5           | 16.9               | 21.2              | 15.3              |
| 51148       | 8.6               |                | 22.1            | 6.5             | 22.1              | 9.6              | 14.1             | 20.3            | 33.2            | 23.6             | 19.6              | 19.7             | 22.2           | 17.3               | 22.0              | 14.5              |
| 51164       | 8.8               | 18.7           | 22.4            | 7.1             | 22.3              | 9.8              | 14.0             | 20.3            | 33.5            | 24.0             | 20.1              | 20.3             | 23.2           | 17.2               | 21.9              | 15.8              |
| 51147       | 9.3               | 18.2           | 22.8            | 7.0             | 22.1              | 8.7              | 14.1             | 20.5            | 33.7            | 23.4             | 19.9              | 20.2             | 22.9           | 17.5               | 21.1              | 16.0              |
| 51165       | 8.6               |                |                 | 7.3             |                   | 9.5              | 13.9             | 20.7            | 33.9            | 23.9             | 20.0              | 20.1             | 22.5           | 16.2               | 21.9              | 16.7              |
| 51156       | 9.0               | 18.6           | 22.1            | 6.6             | 22.8              | 9.4              | 14.2             |                 | 34.2            | 23.6             | 20.1              | 20.1             | 22.8           | 17.3               | 22.2              | 16.0              |
| 51150       | 9.5               | 17.3           | 20.9            | 6.7             | 22.1              | 9.3              | 13.9             | 20.1            | 34.2            | 24.2             |                   | 20.3             | 22.9           | 17.3               | 21.3              | 15.4              |
| 51160       | 8.8               | 18.6           | 21.6            | 6.6             | 23.0              | 9.1              | 13.7             | 20.6            | 34.3            | 24.3             | 20.5              | 20.1             | 22.9           | 17.8               | 21.3              |                   |
| 51167       | 8.7               | 17.9           | 21.5            | 6.5             | 21.6              | 9.3              | 14.4             | 20.3            | 34.4            | 23.0             | 19.9              | 20.2             | 22.8           | 17.1               | 20.9              | 15.8              |
| 51162       | 8.1               | 17.9           | 22.5            | 6.9             | 21.7              | 9.5              | 12.8             | 19.8            | 34.4            | 24.1             | 19.5              | 19.7             | 22.2           | 17.1               | 21.5              | 17.0              |
| 51149       | 8.3               | 17.9           | 21.6            | 6.8             | 22.1              | 9.1              | 13.9             | 21.0            | 34.7            | 24.4             | 20.5              | 20.4             | 22.6           |                    | 21.3              | 16.4              |
| 51146       | 9.3               | 18.8           | 21.8            | 7.2             | 23.3              | 9.4              | 14.1             | 20.4            | 34.9            | 24.2             | 20.0              | 20.6             | 23.0           | 17.7               | 21.8              | 15.6              |
| 51155       | 9.0               | 17.7           | 22.3            | 6.8             | 23.1              | 9.0              | 13.9             | 20.4            | 34.9            | 24.6             | 20.3              | 20.6             | 23.2           | 18.0               | 21.5              | 15.6              |
| 51161       | 9.5               | 19.4           | 23.5            | 8.2             | 23.0              | 9.3              | 13.5             | 20.9            | 35.8            | 25.5             | 20.6              | 20.9             | 23.4           | 17.9               | 22.1              | 16.0              |
| 51145       |                   |                |                 |                 | 21.9              | 9.4              | 14.2             | 20.1            |                 |                  | 19.8              |                  |                | 17.0               |                   | 17.2              |

TABLE 29  
SKELETAL MEASUREMENTS (IN MILLIMETERS) OF MALES OF *brevicauda*

| Num-<br>ber | Width<br>laeoral | Width<br>skull | Length<br>ramus | Height<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula |
|-------------|------------------|----------------|-----------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|
| 48693       | 9 8              | 20 1           | 24 1            | 9 6             | 23 7              | 9 1              | 14 0             | 21 1            | 34 2            | 24 0             | 20 7              | 20 8             | 23 7           | 18 3               | 21 8              | 16 1              |
| 48690       |                  |                | 24 5            | 10 1            | 22 3              | 9 0              | 14 3             | 20 2            |                 | 23 7             | 20 3              | 20 8             | 23 3           | 17 5               | 21 4              | 15 5              |
| 48685       | 9 7              | 20 0           | 23 8            | 9 3             | 21 6              | 8 9              | 13 8             | 20 7            | 34 2            | 24 4             | 20 7              | 20 6             | 23 4           | 17 8               | 21 5              | 17 1              |
| 48708       | 9 2              | 19 8           | 24 0            | 9 3             | 23 4              | 9 4              | 14 2             | 20 9            | 34 6            | 24 2             | 20 5              | 20 8             | 23 3           | 17 5               | 21 7              | 16 1              |
| 48703       | 9 6              | 19 8           | 24 5            | 9 3             | 23 0              | 9 6              | 15 0             | 21 3            |                 | 24 3             | 20 7              | 21 2             | 23 7           | 18 1               | 21 7              | 15 9              |
| 48701       | 10 0             | 20 8           | 25 0            | 9 6             | 22 4              | 9 3              | 14 3             | 20 9            | 34 7            | 24 3             | 20 8              | 21 1             | 23 9           | 17 5               | 21 3              | 15 2              |
| 48707       | 10 4             | 19 7           | 25 4            | 9 8             |                   | 9 7              | 14 0             | 20 9            | 34 8            | 25 1             | 20 7              | 20 4             | 23 1           | 18 0               | 21 6              | 16 2              |
| 48696       | 10 0             | 20 0           |                 | 10 1            | 23 1              | 9 3              | 14 4             | 21 0            | 34 8            | 24 1             | 20 1              | 20 2             | 22 9           | 18 0               | 22 0              | 16 6              |
| 48710       | 9 7              | 20 4           | 25 0            | 9 9             | 22 3              | 9 3              | 14 1             | 20 8            | 34 9            | 25 0             | 20 5              | 21 2             | 24 0           | 18 4               | 22 3              | 16 8              |
| 48669       | 10 1             | 20 4           | 24 7            | 10 0            | 23 2              | 9 3              | 14 4             | 20 4            | 34 9            | 25 0             | 20 8              | 21 2             | 23 9           | 18 3               | 22 3              | 16 7              |
| 48665       | 9 5              | 20 2           | 24 7            | 9 7             | 23 1              | 9 0              | 13 7             | 21 1            | 35 0            | 24 4             | 20 5              | 20 9             | 23 4           | 17 9               | 22 3              | 16 4              |
| 48673       | 10 4             | 20 1           | 24 6            | 10 0            | 23 7              | 9 8              | 14 7             | 21 0            | 35 0            | 25 1             | 20 7              | 21 2             | 23 7           | 18 2               | 21 9              | 16 2              |
| 48689       |                  | 20 2           | 23 8            | 9 6             | 23 7              | 9 4              | 14 8             | 20 9            | 35 0            | 25 0             | 20 9              | 21 0             | 23 6           |                    | 22 6              | 15 3              |
| 48667       |                  |                | 24 7            | 10 0            |                   |                  | 14 0             | 21 3            |                 | 24 6             | 21 1              | 21 2             | 23 9           | 18 8               | 22 7              |                   |
| 48670       |                  |                |                 |                 |                   |                  | 13 8             | 20 3            | 35 4            | 25 2             | 20 9              | 20 9             | 23 8           |                    | 21 9              | 15 5              |
| 48691       |                  | 20 5           | 24 1            | 9 5             | 23 4              | 9 2              | 15 5             | 21 9            | 35 4            | 26 0             | 21 6              | 21 8             | 24 4           | 18 5               | 23 1              | 17 0              |
| 48705       | 10 5             | 20 0           | 24 1            | 9 6             | 23 2              | 9 7              | 14 7             | 21 0            | 35 6            | 24 5             | 20 6              | 21 0             | 23 6           | 18 1               | 22 3              | 16 0              |
| 48709       | 10 0             | 19 9           | 23 3            | 9 2             | 22 2              | 9 4              | 13 8             | 21 2            | 35 6            | 26 0             | 20 9              | 21 6             | 24 1           | 18 3               | 21 8              | 16 1              |
| 48700       | 9 5              |                | 24 4            | 9 2             | 22 6              | 9 7              | 14 8             | 21 6            | 35 7            | 25 4             | 21 0              | 20 8             | 23 6           | 18 2               | 22 4              | 16 2              |
| 48686       | 9 7              | 20 2           | 25 1            | 10 5            | 24 0              | 9 7              | 13 7             | 21 3            | 35 7            | 25 1             | 20 9              | 21 3             | 23 9           | 18 6               | 22 7              | 17 7              |
| 48675       | 9 6              | 20 0           | 24 3            | 9 8             | 22 8              | 8 9              | 14 9             | 21 0            | 35 7            | 25 2             | 20 9              | 20 9             | 23 3           | 18 3               | 22 3              | 16 1              |
| 48666       |                  |                | 25 5            | 9 0             | 23 3              | 9 2              | 14 0             | 21 6            | 35 8            | 25 3             | 21 1              | 21 6             | 24 5           | 18 8               | 23 5              | 17 1              |
| 48697       | 10 0             | 19 4           | 24 8            | 9 6             | 22 1              | 9 9              | 14 1             | 20 6            | 35 8            | 25 1             | 20 2              | 20 9             | 23 2           | 17 8               | 22 0              | 16 5              |
| 48688       | 9 7              | 20 4           | 24 1            | 8 9             | 21 8              | 9 6              | 14 6             | 20 5            | 36 0            | 25 2             | 20 7              | 20 9             | 23 5           | 18 2               | 21 9              | 16 7              |
| 48698       | 10 5             | 20 4           | 25 3            | 9 8             | 23 5              | 9 9              |                  | 21 3            | 36 0            | 25 7             | 21 2              | 21 6             | 24 2           | 18 6               | 22 6              | 16 6              |
| 48690       | 10 4             | 20 4           | 25 2            | 9 8             | 22 8              | 9 2              | 14 8             | 21 1            | 36 1            | 25 1             | 20 7              | 20 4             | 23 2           | 18 3               | 21 9              | 16 6              |
| 48687       | 9 4              | 19 8           | 23 9            | 9 5             | 22 9              | 9 3              | 14 1             | 21 6            | 36 2            | 25 5             | 21 4              | 21 7             | 24 3           | 19 0               | 23 0              | 16 1              |
| 48678       | 10 0             | 20 0           |                 | 9 0             | 22 5              | 9 0              | 14 0             | 21 3            | 36 2            | 25 1             | 21 0              | 21 3             | 24 0           | 18 5               | 21 4              | 16 8              |
| 48677       | 10 3             | 20 3           | 25 7            | 10 6            | 23 8              | 9 7              | 14 7             | 22 0            | 36 5            | 25 7             | 21 5              | 21 5             | 24 1           | 18 3               | 22 3              | 17 0              |
| 48692       | 9 9              | 20 8           | 25 2            | 9 1             | 22 2              | 9 9              | 13 7             | 21 8            | 36 5            | 26 9             | 20 9              | 20 7             | 23 8           | 18 5               | 22 3              | 18 2              |
| 48684       | 9 1              |                | 24 0            | 10 0            | 22 7              | 9 2              | 15 0             | 22 0            | 36 9            | 26 0             | 21 7              | 21 9             | 24 3           | 19 0               | 23 1              | 15 8              |

TABLE 30  
SKELETAL MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF MALES OF *mariposae* M.

| Number | Length<br>radius | Height<br>radius | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula | Weight |
|--------|------------------|------------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|--------|
| 48737  | 22 1             |                  | 22 2              | 9 7              |                  |                 | 31 3            | 22 0             | 19 3              | 19 0             | 21 8           | 16 7               | 21 5              |                   | 26 5   |
| 48726  | 22 4             | 7 7              | 22 0              | 9 3              | 12 0             | 20 7            | 33 3            | 23 9             | 20 3              | 20 5             | 23 2           | 17 1               | 20 8              | 14 8              | 32 2   |
| 48727  | 23 6             | 8 4              | 22 2              | 9 4              | 14 1             | 20 1            | 33 4            | 23 9             | 20 0              | 20 2             | 22 7           | 17 1               | 21 1              | 15 9              | 29 6   |
| 48744  | 23 1             | 7 8              | 21 5              | 9 1              | 13 7             | 20 4            | 33 4            | 23 1             | 20 3              | 20 5             | 23 3           | 17 8               | 21 2              | 15 1              | 26 9   |
| 48754  |                  | 7 5              | 21 5              | 8 9              | 13 1             | 20 0            | 33 4            | 23 6             | 20 3              | 20 1             | 22 7           | 17 3               | 20 7              | 15 3              | 26 5   |
| 48761  | 22 7             | 7 8              | 21 0              | 8 8              | 13 9             | 19 9            | 33 5            | 24 0             | 19 7              | 19 8             | 22 2           | 16 8               | 20 1              | 15 8              | 28 5   |
| 48724  | 22 3             | 8 5              | 22 3              | 8 4              | 13 8             | 19 8            | 33 5            | 23 7             | 20 0              | 20 6             | 23 1           | 16 9               | 21 2              | 15 2              | 29 5   |
| 48731  | 22 8             | 8 7              | 23 3              | 9 5              | 13 9             | 20 3            | 33 6            | 23 1             | 20 2              | 20 2             | 23 1           | 17 9               |                   | 16 6              | 31 9   |
| 48750  | 22 6             | 8 2              | 22 4              | 9 4              | 14 0             | 20 5            | 33 6            | 24 2             | 20 1              | 19 9             | 22 6           | 17 5               | 21 9              | 16 1              | 29 4   |
| 48755  | 23 1             | 7 8              | 21 4              | 8 7              | 13 3             | 20 0            | 33 6            | 23 9             |                   | 20 1             | 22 5           | 17 3               | 20 7              | 15 7              | 29 5   |
| 48745  | 23 3             | 8 1              | 22 5              | 9 3              | 13 2             | 20 4            |                 | 23 9             | 20 4              | 20 5             | 23 0           | 18 2               | 22 0              | 15 9              | 31 0   |
| 48738  | 22 7             | 8 0              | 22 2              | 9 2              | 13 4             | 20 6            |                 | 24 1             | 20 1              | 19 8             | 22 9           | 17 1               | 21 4              | 15 0              | 30 5   |
| 48729  |                  | 8 0              | 21 5              | 9 4              |                  |                 | 33 7            | 23 8             | 19 7              |                  |                | 16 9               | 20 7              | 15 7              | 30 5   |
| 48733  | 24 1             | 8 1              | 22 4              | 9 7              | 14 1             | 20 7            | 33 7            | 24 1             | 19 9              | 19 9             | 22 7           | 17 4               | 21 2              | 15 9              | 30 4   |
| 48751  | 21 8             |                  |                   | 8 9              | 13 7             | 20 1            | 33 7            | 23 6             | 19 7              | 20 1             | 22 9           | 17 8               | 21 3              | 14 9              | 30 8   |
| 48736  | 22 3             | 8 5              | 22 3              | 8 6              | 13 0             | 20 7            | 33 8            | 24 2             | 20 2              | 20 4             | 23 1           | 17 5               | 21 3              | 15 8              | 30 5   |
| 48741  | 23 5             | 8 4              | 22 2              | 9 2              |                  | 20 5            | 33 9            | 23 8             | 19 8              | 20 3             | 22 7           | 17 4               | 21 6              | 15 3              | 29 7   |
| 48717  | 22 3             | 8 4              | 23 0              | 9 5              | 12 2             | 20 3            | 33 9            | 23 9             | 20 0              | 20 3             | 23 0           | 17 8               | 22 0              |                   | 31 0   |
| 48762  | 22 5             | 8 3              | 22 1              | 9 0              | 14 3             |                 | 34 0            | 23 6             |                   | 20 4             | 23 1           | 17 5               |                   | 16 2              | 30 5   |



TABLE 30—(Continued)

| Number | Length<br>ramus | Height<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula | Weight |
|--------|-----------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|--------|
| 48723  | 22 3            | 7 6             | 21 5              | 8 6              | 13 0             | 20 4            | 34 1            | 23 9             | 20 4              | 20 4             | 22 9           | 17 3               | 21 0              | 15 3              | 29 8   |
| 48718  | 23 6            | 8 2             | 22 3              | 9 3              |                  | 20 6            | 34 2            | 24 3             | 20 3              | 20 2             | 23 2           | 17 5               | 21 8              | 16 2              | 32 0   |
| 48747  | 23 1            | 7 8             | 22 1              | 9 2              | 13 0             | 20 6            | 34 2            | 24 6             | 20 4              | 20 3             | 23 3           | 17 4               | 20 8              | 15 3              | 28 8   |
| 48756  |                 | 9 2             | 22 2              | 9 5              | 13 2             | 19 6            | 34 2            | 24 1             | 19 7              | 19 8             | 22 7           | 17 5               | 20 9              | 15 1              | 30 7   |
| 48753  | 23 2            | 7 9             | 21 9              | 8 8              | 13 1             | 20 9            | 34 3            | 24 2             | 20 8              | 20 3             | 23 3           | 18 0               | 20 7              | 17 3              | 34 0   |
| 48730  | 22 9            | 8 2             | 22 2              | 9 3              | 12 7             | 20 7            | 34 4            | 24 3             | 20 5              | 20 7             | 23 3           | 17 8               | 21 0              | 15 7              | 30 4   |
| 48746  | 23 7            | 8 7             | 23 3              | 9 3              | 13 3             | 20 2            | 34 4            | 23 8             | 20 1              | 20 5             | 23 3           | 18 0               | 22 5              | 15 0              | 32 2   |
| 48720  | 23 1            | 8 3             | 22 7              | 9 4              | 12 9             | 21 2            |                 | 24 5             | 20 7              | 21 1             | 23 7           | 18 5               | 21 4              | 16 2              | 31 7   |
| 48714  | 22 9            | 8 3             | 23 9              | 9 5              | 13 4             | 20 6            | 34 6            | 24 6             | 20 4              | 20 4             | 23 2           | 17 8               | 21 4              | 16 3              | 32 0   |
| 48735  | 22 7            | 7 9             | 21 8              | 9 7              | 13 3             | 20 9            | 34 6            | 24 8             | 20 3              | 20 3             | 23 2           | 17 7               | 21 5              | 16 1              | 30 3   |
| 48759  | 23 4            | 7 8             | 22 1              | 9 5              | 14 0             | 20 3            | 34 6            | 24 1             | 19 9              | 20 2             | 23 1           | 17 5               | 21 4              | 15 9              | 32 2   |
| 48743  | 23 5            | 8 7             | 22 2              | 9 2              |                  | 20 0            | 34 8            | 24 7             | 20 2              | 21 1             | 23 6           | 17 2               | 21 0              | 15 5              | 30 7   |
| 48765  | 23 5            | 8 3             | 22 7              | 8 7              | 14 1             | 20 9            | 35 1            | 25 5             | 20 7              | 21 6             | 24 0           | 18 1               | 21 8              | 15 8              | 30 8   |
| 48739  | 23 1            | 8 2             | 22 8              | 9 6              | 14 0             | 20 6            | 35 2            | 25 1             | 20 2              | 20 4             | 23 0           |                    | 22 3              | 15 0              | 32 2   |
| 48728  | 24 4            | 8 9             | 22 1              | 9 5              | 14 4             | 21 1            | 35 3            | 24 6             | 20 7              | 20 5             | 23 3           | 17 3               | 22 5              | 16 1              | 32 0   |
| 48722  | 23 6            | 8 6             | 23 3              | 9 4              | 14 0             | 21 2            | 35 5            | 25 4             | 20 7              | 21 1             | 23 8           | 17 8               | 22 4              | 16 2              | 31 5   |
| 48725  |                 |                 | 21 2              | 8 7              | 13 8             | 20 9            | 35 5            | 25 1             | 20 0              | 20 3             | 23 4           | 17 9               | 21 7              | 15 5              | 31 2   |
| 48758  | 23 3            | 8 0             | 23 1              | 9 5              | 14 2             | 20 4            | 35 5            | 25 2             | 20 0              | 20 7             | 23 3           | 17 7               | 23 2              | 15 0              | 34 7   |
| 48721  | 22 9            | 8 4             | 22 3              | 10 0             | 14 2             | 21 0            | 36 0            | 25 0             | 20 2              | 21 1             | 23 5           | 18 1               | 21 7              | 14 8              | 32 1   |

TABLE 31  
SKELETAL MEASUREMENTS (IN MILLIMETERS) OF MALES OF *mariposae* FROM LAKE TAHOE

| Num-<br>ber | Width<br>lacrima | Width<br>skull | Length<br>ramus | Height<br>ramus | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furcula |
|-------------|------------------|----------------|-----------------|-----------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|
| 50709       | 8 8              |                | 23 3            | 7 8             | 22 8              | 9 0              | 14 0             | 19 8            | 32 7            | 23 2             | 20 0              | 20 1             | 22 5           | 16 9               | 21 5              | 15 1              |
| 50717       |                  |                |                 |                 |                   |                  | 14 1             | 20 3            | 33 0            | 23 4             | 20 1              | 19 9             |                | 17 4               | 21 3              | 16 1              |
| 50726       | 9 3              | 19 0           | 22 4            | 8 3             | 21 9              | 8 7              | 12 2             | 19 5            | 33 1            | 23 1             | 19 7              | 19 0             | 22 0           | 17 0               | 21 9              | 14 5              |
| 50700       | 9 2              | 19 0           | 21 9            | 8 2             | 22 1              | 9 5              | 13 4             | 19 6            | 33 1            | 23 5             | 19 5              | 20 0             | 22 4           | 17 1               | 21 3              | 16 3              |
| 50689       | 9 1              | 18 3           | 23 2            | 8 5             | 22 6              | 9 1              | 13 9             | 19 4            | 33 3            | 23 5             | 19 4              | 19 5             | 22 0           | 16 8               | 21 5              | 15 9              |
| 50681       | 9 0              | 18 8           | 22 0            | 8 1             | 22 0              | 9 3              | 14 4             | 20 4            | 33 5            | 23 6             | 20 1              | 20 1             | 22 8           | 17 2               |                   | 15 5              |
| 50707       | 8 9              | 17 9           | 21 6            | 7 6             | 21 4              | 9 6              | 13 7             | 19 6            | 33 6            | 23 4             | 19 9              | 20 4             | 23 0           | 17 5               | 21 8              | 16 2              |
| 50731       | 9 1              | 20 0           | 22 9            | 8 5             | 23 3              | 8 7              | 14 8             | 20 3            | 33 7            | 24 2             | 20 3              | 20 8             | 23 3           | 17 7               | 22 1              | 16 0              |
| 50690       | 9 4              | 18 8           | 23 1            | 8 4             | 22 3              | 9 0              | 13 3             | 20 3            | 33 9            | 24 6             | 20 4              | 20 2             | 22 9           | 17 7               | 21 0              | 15 8              |
| 50696       | 9 3              | 19 0           | 23 2            | 7 6             | 23 0              | 10 1             | 14 0             | 20 3            | 33 9            | 23 8             | 20 3              | 20 0             | 22 5           | 17 7               | 22 2              | 16 9              |
| 50685       | 9 8              | 18 8           | 21 9            | 8 6             | 22 5              | 9 4              | 14 2             | 20 1            | 34 0            | 24 1             | 20 3              | 20 3             | 23 0           | 17 4               | 21 6              | 16 4              |
| 50678       | 8 9              |                |                 | 7 3             | 21 7              | 9 9              | 13 0             | 20 0            | 34 1            | 23 8             | 19 9              | 20 5             | 22 9           | 17 5               | 22 0              |                   |
| 50702       | 9 0              | 19 1           |                 | 7 8             | 21 5              | 8 8              | 13 6             | 20 3            | 34 1            | 24 1             | 19 8              | 19 7             | 22 2           | 17 1               | 21 0              | 16 5              |
| 50699       | 8 8              |                | 23 3            | 8 9             | 22 1              |                  | 13 0             | 20 2            | 34 1            | 24 4             | 19 5              | 19 4             | 21 9           | 16 6               | 21 6              | 16 2              |
| 50694       | 9 0              |                | 22 0            | 8 3             | 22 1              | 9 5              | 13 7             | 20 5            | 34 1            | 24 6             | 19 6              | 19 8             | 22 2           | 17 2               | 21 2              | 15 0              |
| 50708       | 8 7              | 19 1           |                 |                 | 22 7              | 9 3              |                  | 20 1            | 34 2            | 24 0             | 20 0              | 19 9             | 22 5           | 16 9               | 20 7              | 15 4              |
| 50719       | 8 8              |                | 22 7            | 8 4             | 20 9              | 8 8              | 13 7             | 20 7            | 34 3            | 23 8             | 20 5              | 20 4             |                | 17 1               | 20 9              | 15 6              |
| 50727       | 8 9              | 18 9           | 22 5            | 8 4             | 21 2              | 9 1              | 14 0             | 19 9            | 34 4            | 24 0             | 19 6              | 20 0             | 22 8           | 15 7               | 20 4              |                   |
| 50698       | 9 3              |                | 23 9            | 8 5             | 22 4              | 8 9              | 14 7             | 20 1            | 34 4            | 24 8             | 20 0              | 20 7             | 23 1           | 18 8               | 21 3              | 16 5              |

TABLE 31—(Continued)

| Num-<br>ber | Width<br>lacrimal | Width<br>skull | Length<br>radius | Height<br>radius | Length<br>sternum | Width<br>sternum | Length<br>pelvis | Length<br>femur | Length<br>tibia | Length<br>tarsus | Length<br>humerus | Length<br>radius | Length<br>ulna | Length<br>coracoid | Length<br>scapula | Length<br>furella |
|-------------|-------------------|----------------|------------------|------------------|-------------------|------------------|------------------|-----------------|-----------------|------------------|-------------------|------------------|----------------|--------------------|-------------------|-------------------|
| 50725       | 9 3               | 18 8           | 22 8             | 8 3              | 22 1              | 9 2              | 12 5             | 20 6            | 34 9            | 24 8             | 20 1              | 20 9             | 23 4           | 17 5               | 21 0              | 16 0              |
| 50732       | 9 3               |                | 22 9             | 8 1              | 21 2              | 9 6              | 13 9             | 20 6            | 35 0            | 24 0             | 20 5              | 20 7             | 23 4           | 17 6               | 21 0              | 15 1              |
| 50687       | 9 3               | 19 3           | 23 1             | 8 5              | 21 9              | 9 1              | 13 2             | 20 5            | 35 0            | 24 7             | 20 0              | 20 8             | 23 2           | 17 8               | 21 0              | 15 7              |
| 50691       | 9 0               | 18 2           |                  | 8 6              | 23 2              | 9 8              |                  | 20 7            | 35 1            | 24 5             | 20 4              | 20 7             | 23 5           | 17 7               | 21 7              | 16 2              |
| 50730       | 9 0               | 19 1           | 22 7             | 7 9              | 22 5              | 10 7             |                  |                 | 35 1            | 24 5             | 20 6              | 21 3             | 23 9           | 17 9               | 22 6              | 15 7              |
| 50714       | 9 5               | 19 3           | 23 3             | 8 4              | 23 5              | 8 8              | 13 3             | 20 5            | 35 1            | 25 1             | 20 5              | 20 8             | 23 5           | 17 8               | 22 2              | 16 0              |
| 50710       | 9 4               | 19 4           | 22 9             | 8 5              | 22 9              | 9 2              | 13 6             | 20 8            | 35 2            | 24 1             | 20 5              | 20 4             | 23 1           | 17 6               | 21 7              | 17 2              |
| 50705       | 8 9               |                | 24 2             | 8 5              | 22 9              | 9 3              |                  | 21 1            | 35 2            | 25 5             | 20 6              | 21 3             | 23 9           | 17 7               | 21 8              | 15 9              |
| 50723       | 9 3               |                | 22 8             | 8 6              | 22 0              | 9 2              | 14 3             | 20 5            | 35 3            | 24 6             | 20 1              | 20 1             | 22 7           | 17 5               | 21 3              | 16 0              |
| 50712       | 9 1               |                | 23 9             | 8 9              | 23 4              | 9 3              | 13 9             | 21 3            | 35 6            | 24 8             | 20 6              | 20 7             | 23 6           | 18 4               | 22 5              | 16 9              |
| 50715       | 9 2               | 19 0           | 24 1             | 8 3              | 22 4              | 9 0              | 14 1             | 20 9            | 35 7            | 24 8             | 20 9              | 21 0             | 23 8           | 18 2               | 21 5              | 16 5              |
| 50693       | 8 9               | 20 0           | 22 9             | 8 7              | 23 0              | 9 7              | 15 1             | 21 3            | 36 1            | 24 8             | 20 9              | 21 0             | 23 7           | 18 1               | 21 5              | 16 9              |
| 50703       | 9 7               | 19 1           | 24 3             | 9 3              | 22 3              | 9 3              | 14 1             | 21 7            | 36 3            | 26 3             | 21 0              | 21 0             | 24 0           | 17 9               | 22 3              | 17 1              |
| 50701       | 9 0               | 18 4           | 22 6             | 8 1              | 22 4              | 9 1              |                  |                 |                 |                  | 19 7              | 19 9             | 22 5           | 17 3               | 20 4              | 15 4              |
| 50686       | 9 3               |                | 22 4             | 8 2              |                   |                  | 13 7             | 20 6            |                 | 23 9             |                   | 19 8             | 22 4           | 17 3               |                   |                   |
| 50729       |                   | 18 6           | 22 4             | 8 2              |                   |                  |                  | 20 9            |                 | 24 9             | 20 3              | 20 4             | 23 3           | 17 7               | 20 2              | 15 2              |
| 50680       | 8 6               |                |                  |                  |                   |                  |                  |                 |                 | 24 1             |                   | 20 3             | 23 1           |                    |                   |                   |

## LITERATURE CITED

- ALLEN, A. S.  
1915. Birds of a Berkeley hillside. *Condor*, 17, 78-85.  
1920. The rusty song sparrow in Berkeley, and the return of winter birds. *Condor*, 22, 16-18.
- ALLEN, J. A.  
1871. On the mammals and winter birds of east Florida. *Bull. Mus. Comp. Zool.*, 2, 161-450.  
1898. "A precise criterion of species." *Science*, n. s., 7, 801-2.
- AMERICAN ORNITHOLOGISTS' UNION COMMITTEE.  
1910. Check-list of North American birds (ed. 3, revised; New York, American Ornithologists' Union), 430 pp., 2 maps.
- ARNOLD, E.  
1912. A short summer outing in Newfoundland, 1911. *Auk*, 29, 72-79.
- BAILEY, F. M.  
1902. Handbook of birds of the Western United States (Boston and New York, Houghton, Mifflin and Company), xcii + 512 pp., 601 figs. in text, 33 pls.
- BAIRD, S. F. (with the cooperation of CASSIN, J., AND LAWRENCE, G. N.).  
1858. Birds. *Pacific Railroad Reports*, 9, lvi + 1005 pp.
- BARLOW, C.  
1901. A list of the land birds of the Placerville-Lake Tahoe stage road. *Condor*, 3, 151-84.
- BARROWS, W. B.  
1912. Michigan bird life (Mich. Agr. College), xiv + 822 pp.
- BEAN, T. H.  
1882. Notes on birds collected during the summer of 1880, in Alaska and Siberia. *Proc. U. S. Nat. Mus.*, 5, 144-73.
- BEDDARD, F. E.  
1898. The structure and classification of birds (London, Longmans), xx + 548 pp., 252 figs. in text.
- BELDING, L.  
1903. Curious trait of thick-billed sparrow. *Condor*, 5, 79.
- BENDIRE, C. E.  
1889. Notes on the general habits, nests and eggs of the genus *Passerella*. *Auk*, 6, 107-16.
- BREWSTER, W.  
1906. The birds of the Cambridge region of Massachusetts. *Mem. Nutt. Ornith. Club*, no. 4, 426 pp., 4 pls. 3 maps.
- BROWN, W. J.  
1911. Some Newfoundland bird notes—May, June, July, 1911. *Ottawa Nat.*, 25, 89-94.  
1912. Additional notes on the birds of Newfoundland. *Ottawa Nat.*, 26, 93-98.
- BRYANT, H. C.  
1911. The relation of birds to an insect outbreak in northern California during the spring and summer of 1911. *Condor*, 13, 195-208.

BUMPUS, H. C.

1897. The variations and mutations of the introduced sparrow. *Biol. Lect. Woods Holl*, 1896, 1-15.

CHANEY, R. W.

1910. Summer and fall birds of the Hamlin Lake region, Mason County, Michigan. *Auk*, 27, 271-79.

CHAPIN, J. P.

1924. Size-variation in *Pyrenestes*, a genus of weaver-finches. *Bull. Am. Mus. Nat. Hist.*, 49, art. 4, pp. 415-41.

CHAPMAN, F. M.

1920. Unusual types of apparent geographic variation in color and of individual variation in size exhibited by *Ostinops decumanus*. *Proc. Biol. Soc. Wash.*, 33, 25-32.

1923. Mutation among birds in the genus *Buarremon*. *Bull. Am. Mus. Nat. Hist.*, 48, art. 9, pp. 243-78.

CHAPMAN, F. M., AND GRISCOM, L.

1924. House wrens of the genus *Troglodytes*. *Bull. Am. Mus. Nat. Hist.*, 50, 279-304.

COOK, W. W.

1888. Report on bird migration in the Mississippi Valley in the years 1884 and 1885. *U. S. Dept. Agr., Div. Econ. Ornith., Bull.* 2, 313 pp.

COUES, E.

1874. Birds of the northwest: a hand-book of the ornithology of the region drained by the Missouri River and its tributaries. *U. S. Geol. Surv. Terr., Misc. Publ.*, 3, xi + 791 pp.

DAWSON, W. L.

1903. The birds of Ohio (Columbus, Wheaton), 1, xlv + 368, many illus.

DAVENPORT, C. B.

1898. A precise criterion of species. *Science*, n. s., 7, 685-90.

DICE, L. R.

1920. Notes on some birds of interior Alaska. *Condor*, 22, 176-85.

DWIGHT, J.

1900. The sequence of plumages and moults of the passerine birds of New York. *Ann. New York Acad. Sci.*, 13, no. 1, pp. 73-360.

1925. The gulls (Laridae) of the world; their plumages, moults, variations, relationships and distribution. *Bull. Am. Mus. Nat. Hist.*, 52, 63-401.

DWIGHT, J., AND GRISCOM, L.

1921. A revision of *Atlapetes gutturalis* with descriptions of three new races. *Am. Mus. Novitates*, no. 16, Sept. 9, 1921, 4 pp.

EATON, E. H.

1914. Birds of New York. *Mem.* 12, New York State Mus., pt. 2, pp. 1-719, many illus.

EIFRIG, C. W. G.

1910. Stomach contents of some Canadian birds. *Ottawa Naturalist*, 24, 18-20.

ENGLISH, T. M. S.

1923. On the greater length of the day in higher latitudes as a reason for spring migration. *Ibis*, 11, series 5.

FORBUSH, E. H.

1908. Useful birds and their protection. Mass. State Board Agr., xx + 437 pp.

FROST, F.

1927. Statistical identification as applied to *Parapavo*. Univ. Calif. Publ. Bull. Geol. Sci., 17, 57-62.

GARRETT, H. E.

1926. Statistics in psychology and education (New York, Longmans, Green and Co.), xiii + 317 pp., many tables and diagrams.

GATES, R. R.

1917. The mutation theory and the species concept. Am. Nat., 51, 577-95.

GOSS, N. S.

1891. History of the birds of Kansas (Topeka, Crane and Company), 692 pp., many illus.

GRINNELL, J.

1900. Birds of the Kotzebue Sound region, Alaska. Pacific Coast Avifauna, 1, 80, 1 map.
1905. Summer birds of Mount Pinos, California. Auk, 22, 378-91.
1908. The biota of the San Bernardino Mountains. Univ. Calif. Publ. Zool., 5, 1-170, 24 pls.
- 1909a. Birds and mammals of the 1907 Alexander expedition to south-eastern Alaska. *Ibid.*, 5, 171-264, pls. 25-26, 4 figs. in text.
- 1909b. A new cowbird of the genus *Molothrus*. *Ibid.*, 5, 275-81, 6 figs. in text.
1910. Birds of the 1908 Alexander Alaska expedition, with a note on the avifaunal relationships of the Prince William Sound district. *Ibid.*, 5, 361-428, pls. 33-34, 9 figs. in text.
1914. An account of the mammals and birds of the Lower Colorado Valley with especial reference to the distributional problems presented. *Ibid.*, 12, 51-294, pls. 3-13, 9 figs. in text.
1922. A geographical study of the kangaroo rats of California. *Ibid.*, 24, 1-124, pls. 1-7, 24 figs. in text.
1926. Geography and evolution in the pocket gopher. Univ. Calif. Chronicle, July, 1926, pp. 247-62.

GRINNELL, J., AND SWARTH, H. S.

1913. Birds and mammals of the San Jacinto area of southern California, with remarks upon the behavior of geographic races on the margins of their habitats. Univ. Calif. Publ. Zool., 10, 197-406, pls. 6-10, 3 figs. in text.
1926. New subspecies of birds (*Penthestes*, *Bacolophus*, *Psaltiriparus*, *Chamaea*) from the Pacific coast of North America. *Ibid.*, 30, 163-75.

GRINNELL, J., AND WYTHE, M. W.

1927. Directory to the bird life of the San Francisco Bay region. Pacific Coast Avifauna, 18, 160, 1 map and colored frontispiece.

GRISCOM, L.

1926. Notes on the summer birds of the west coast of Newfoundland. *Ibis*, pp. 656-84.

GROSS, A. O.

1921. The dickcissel (*Spiza americana*) of the Illinois prairies. Auk, 38, 1-26, 163-84.

HANNA, W. C.

1924. Weights of about three thousand eggs. *Condor*, 28, 146-53.

HEATH, H.

1915. Birds observed on Forrester Island, Alaska, during the summer of 1913. *Condor*, 17, 20-41.

HOWELL, A. B.

1924. Individual and age variation in *Microtus montanus yosemitic*. *Jour. Agr. Res.*, 28, 977-1015.

INGERSOLL, A. M.

1913. Great destruction of birds' eggs and nestlings in the Sierra Nevada. *Condor*, 15, 81-86.

JONES, L.

1910. The birds of Cedar Point and vicinity. *Wilson Bull*, 22, 97-115.

JORDAN, D. S.

1927. Review of Studies of the variation, distribution and evolution of the genus *Partula*; the species inhabiting Tahiti, by Henry Edward Crampton. *Science*, n. s., 65, 186-87.

JUDD, S. O.

1901. The relation of sparrows to agriculture. U. S. Dept. Agr. Div. Biol. Surv., Bull. No. 5, 98 pp., 4 pls., 98 figs. in text.

KEELER, C. A.

1890. Song birds about San Francisco Bay. *Zoe*, 1, 116-20.

KEYES, C. R.

1905. Some bird notes from the central Sierras. *Condor*, 7, 13-17.

KOPMAN, H. H.

1915. List of birds of Louisiana. Pt. 6. *Auk*, 32, 15-29.

LUCAS, F. A.

1893. A neglected branch of ornithology. *Auk*, 10, 210.

MACFARLANE, R.

1891. Notes on and list of birds and eggs collected in arctic America, 1861-1866. *Proc. U. S. Nat. Mus.*, 14, 413-46.

MACOUN, J., AND MACOUN, J. M.

1909. Catalogue of Canadian birds. *Canad. Dept. Mines, Geol. Surv. Branch*, 761 pp.

MAILLIARD, J. W.

1921. Notes on the nesting of the Yosemite fox sparrow, calliope hummingbird and western wood pewee at Lake Tahoe, California. *Condor*, 23, 73-77.

MAILLIARD, J.

1912. *Passerella stephensi* in Marin County, California. *Condor*, 14, 63-67.

1921. Notes on fox sparrows in California in the autumn of 1921. *Ibid.*, 24, 48-53.

1924. A wintering ground of the Yolla Bolly fox sparrow. *Ibid.*, 26, 112-14.

MEINERTZHAGEN, R.

1926. Introduction to a review of the genus *Corvus*. *Novitates Zoologicae*, 33, 57-121.

MERRIAM, F. A.

1889. Birds through an opera glass (New York, Houghton, Mifflin and Company), 225 pp.

MILLER, L. H.

1912. Contributions to avian paleontology from the Pacific coast of North America. Univ. Calif. Publ. Geol. Sci., 7, 61-115.

MORGAN, T. H.

1923. The bearing of Mendelism on the origin of species. Sci. Monthly, 16, 236-46.

MUNRO, J. A.

1925. Further bird notes from southern Vancouver Island. Canad. Field-Nat., 39, 156-58.

NELSON, E. W.

1887. Report upon natural history collections made in Alaska between the years 1877 and 1881. Arctic Series of Publications issued in connection with the Signal Service, U. S. Army, 3, 337 pp., 21 pls.

NEWTON, A.

- 1893-1896. A dictionary of birds (London, Adam and Charles Black), xii + 1088 pp.

OSGOOD, W. H.

1909. Biological investigations in Alaska and Yukon territory. U. S. Dept. Agr. Bur. Biol. Surv., N. Am. Fauna, 30, 96 pp., 5 pls., 2 figs. in text.

PEARL, R.

1927. The graphic representation of relative variability. Science, n. s., 65, 237-41.

PHILIPP, P. B.

1925. Notes on some summer birds of the Magdalen Islands. Canad. Field-Nat., 39, 75-78.

PIERCE, W. M.

1921. Nesting of the Stephens fox sparrow. Condor, 23, 80-85.

PREBLE, E. A.

1908. A biological investigation of the Athabaska-Mackenzie region. U. S. Dept. Agr., Bur. Biol. Surv., N. Am. Fauna, 27, 574 pp., 25 pls., 16 figs. in text.

PYCRAFT, W. P.

1910. A history of birds (London, Methuen and Company), xxx + 458 pp., 37 pls., 50 figs. in text.

RACEY, K.

1926. Notes on the birds observed in the Alta Lake region, B. C. Auk, 43, 319-25.

RIDGWAY, R.

1878. Song birds of the west. Harpers New Monthly Magazine, 56, 857-80.  
1901. The birds of North and Middle America. U. S. Nat. Mus., Bull. 50, part 1, xxx + 715 pp., 20 pls.

RILEY, J. H.

1912. Birds collected or observed on the expedition of the Alpine Club of Canada to Jasper Park, Yellowhead Pass, and Mount Robson region. The Canadian Alpine Journal, special number, pp. 47-75, 1 pl.

SAUNDERS, A. A.

1910. Singing of the female slate-colored fox sparrow. Condor, 12, 80.  
1911. A preliminary list of the birds of Gallatin County, Montana. Auk, 28, 26-49.



## SHUFELDT, R. W.

1887. Individual variation in the skeletons of birds, and other matters. *Auk*, 4, 265-68, 2 figs. in text. (Letter to editor.)
1888. The osteology of *Habia melanocephala* with comparative notes upon the skeletons of certain other conirostral birds and of the tanagers. *Ibid.*, 5, 438-44, 2 figs. in text. (Letter to editor.)

## SMITH, A. P.

1915. Birds of the Boston Mountains, Arkansas. *Condor*, 17, 41-57.

## SNODGRASS, R. E.

1902. The relation of the food to the size and shape of the bill in the Galapagos genus *Geospiza*. *Auk*, 19, 367-81.
1903. Notes on the anatomy of *Geospiza*, *Cocornis*, and *Certhidia*. *Ibid.*, 20, 402-17.

## STEARNS, W. A.

1883. New England bird life: a manual of ornithology. (Boston, Lee and Shepard), 2 vols., many illus.

## STONE, W.

1908. The birds of New Jersey. Ann. Rept. New Jersey State Mus., pp. 13-347.
1921. Swarth on fox sparrows (review). *Auk*, 38, 133-34.

## STRONG, R. M.

1901. A quantitative study of variation in the smaller North-American shrikes. *Am. Nat.*, 35, 271-98.

## SUMNER, F. B.

1923. Some facts relevant to a discussion of the origin and inheritance of specific characters. *Am. Nat.*, 57, 238-54.
1926. An analysis of geographic variation in mice of the *Peromyscus polionotus* group from Florida and Alabama. *Jour. Mammalogy*, 7, 149-84.

## SURFACE, H. A.

1913. Some Pennsylvania birds and their economic value. *Zool. Bull. Div. Zool.*, Pa. Dept. Agr., 3, 155-216.

## SUSHKIN, P. P.

1925. The American Grosbeak (*Hesperiphona*) the only American genus of a Palaearctic group. *Auk*, 42, 256-61.

## SWARTH, H. S.

1912. Report on a collection of birds and mammals from Vancouver Island. *Univ. Calif. Publ. Zool.*, 10, 1-124, pls. 1-4.
1914. California forms of *Psaltiriparus*. *Auk*, 31, 499-526.
1918. The Pacific coast jays of the genus *Aphelocoma*. *Univ. Calif. Publ. Zool.*, 17, 405-22, 1 fig. in text.
1920. Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. *Ibid.*, 21, 75-224, pls. 4-7, 30 figs. in text.
1923. The systematic status of some northwestern song sparrows. *Condor*, 25, 214-23.
1924. Birds and mammals of the Skeena River region of Northern British Columbia. *Univ. Calif. Publ. Zool.*, 24, 315-94, pls. 9-11, 1 fig. in text.

SWAINSON, W.

- 1836 [1837]. On the natural history and classification of birds (London, Longmans), 2, vi + 398; many figs. in text.

TAVERNER, P. A.

1919. The birds of the Red Deer River, Alberta. *Auk*, 36, 1-21, 248-65.

1921. Swarth on the fox sparrows. *Canad. Field-Nat.*, 35, 76-78.

TAYLOR, H. R.

1891. Nesting habits of thick-billed sparrows. *Zoe*, 2, 123.

TAYLOR, W. P.

1912. Field notes on amphibians, reptiles and birds of northern Humboldt County, Nevada. *Univ. Calif. Publ. Zool.*, 7, 319-436, pls. 7-12.

THOMPSON, A. L.

1926. Problems of bird migration (London, H. F. and G. Witherby). 350 pp.

TOWNSEND, C. W.

1920. Supplement to the birds of Essex County, Massachusetts. *Mem. Nutt. Ornith. Club*, no. 5.

TOWNSEND, C. W., AND ALLEN, G. M.

1907. Birds of Labrador. *Proc. Boston Soc. Nat. Hist.*, 33, 277-428, pls. 1-29.

WALKER, A.

1917. Some birds of central Oregon. *Condor*, 19, 131-40.

WHITTLE, C. L.

1926. On the nature of the relationship existing among land birds during sustained aerial migration. *Auk*, 43, 493-500.

WIDMANN, O.

1896. The peninsula of Missouri as a winter home for birds. *Auk*, 13, 216-22.

WILLETT, G.

1914. Birds of Sitka and vicinity, southeastern Alaska. *Condor*, 16, 71-91.

1915. Summer birds of Forrester Island, Alaska. *Auk*, 32, 295-305.

1920. Additional notes on the avifauna of Forrester Island, Alaska. *Condor*, 22, 138-39.

1921. Distribution of Townsend fox sparrows. *Ibid.*, 23, 36-37.

WOOD, N. A.

1911. The results of the Mershon expedition to the Charity Islands, Lake Huron. *Wilson Bull.*, pp. 78-112.

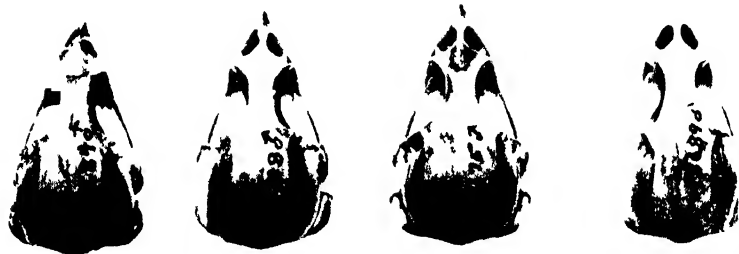
*Transmitted October 18, 1927.*

## EXPLANATION OF PLATES

### PLATE 16

Sixteen skulls of *Passerella iliaca brevicauda* showing individual and sexual variation in a series of skulls from one locality. Rows *a* and *b* are males. Rows *c* and *d* are females.

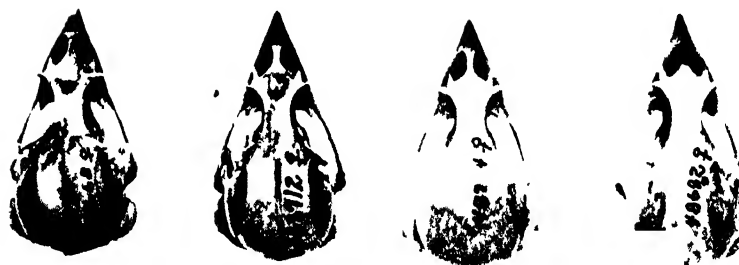
*a*



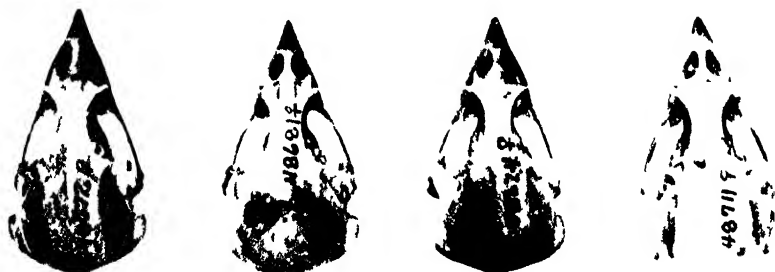
*b*



*c*



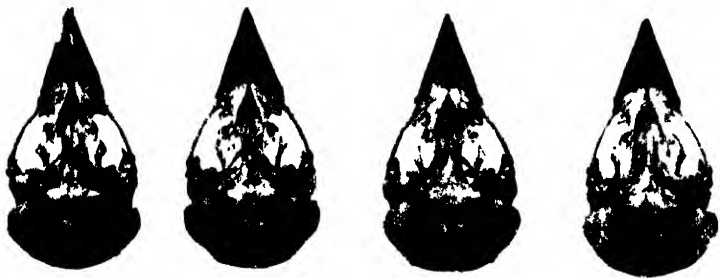
*d*



## PLATE 17

Ventral views of sixteen skulls of *Passerella iliaca brevicauda* showing individual and sexual variation in a series of skulls from one locality. Same skulls as shown in plate 16 and arranged in same order. Rows *a* and *b* are males. Rows *c* and *d* are females.

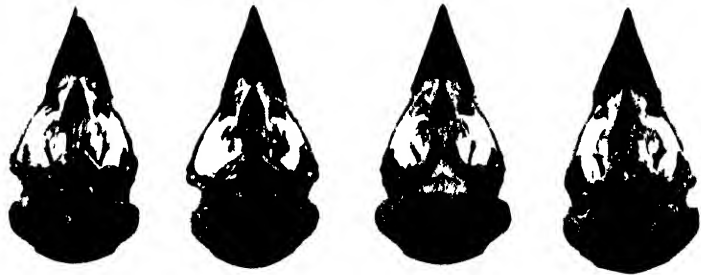
*a*



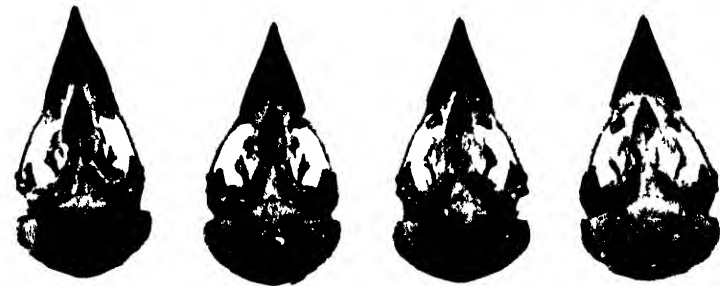
*b*



*c*



*d*



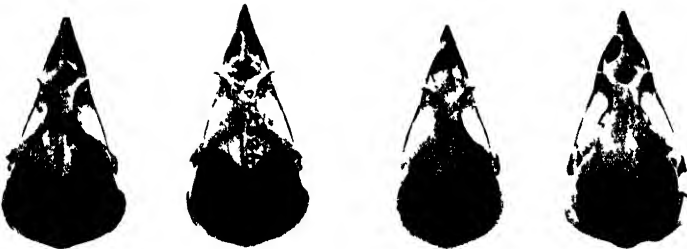
## PLATE 18

Dorsal views of sixteen skulls of *Passerella iliaca* showing geographic variation. In row *a* from left to right are skulls of *iliaca*, *unalaschensis*, *sinuosa*, and *annectans*; row *b*, *townsendi*, *fuliginosa*, *schistacea* (♀), and *fulva*; row *c*, *breviceauda*, *canescens*, *monoensis*, and *mariposae* (Manzanita Lake); row *d*, *mariposae* (Lake Tahoe), *mariposae* (Shaver), *stephensi* (Hume), and *stephensi* (Mount Pinos).

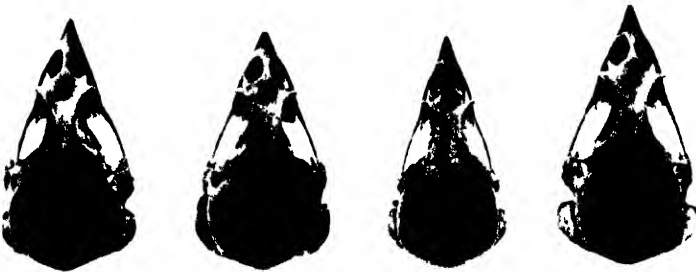
*a*



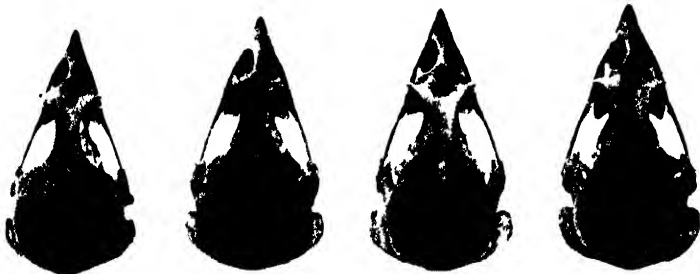
*b*



*c*



*d*

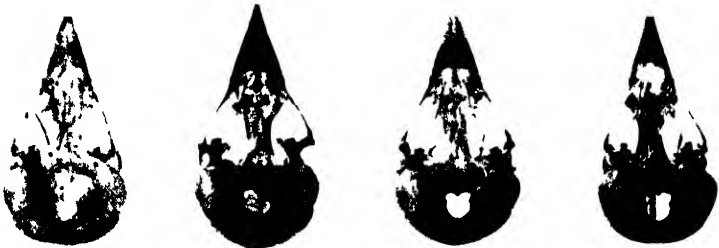




## PLATE 19

Ventral views of sixteen skulls of *Passercella iliaca* showing geographic variation. Same skulls as shown in plate 18 and arranged in same order. In row *a* from left to right are skulls of *iliaca*, *unalaschensis*, *sinuosa*, and *annectens*; row *b*, *townsendi*, *fuliginosa*, *schistacea* (♀), and *fulva*; row *c*, *brevicauda*, *caneceens*, *monoensis*, and *mariposae* (Manzanita Lake); row *d*, *mariposae* (Lake Tahoe), *mariposae* (Shaver), *stephensi* (Hume), and *stephensi* (Mount Pinos).

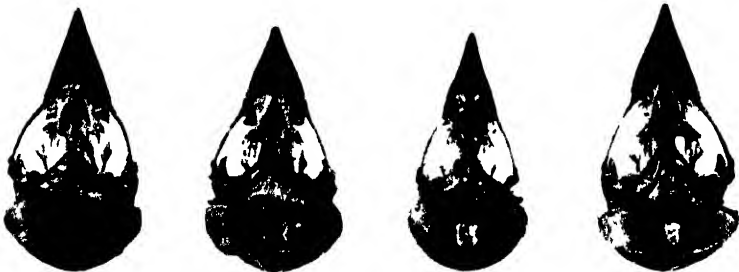
*a*



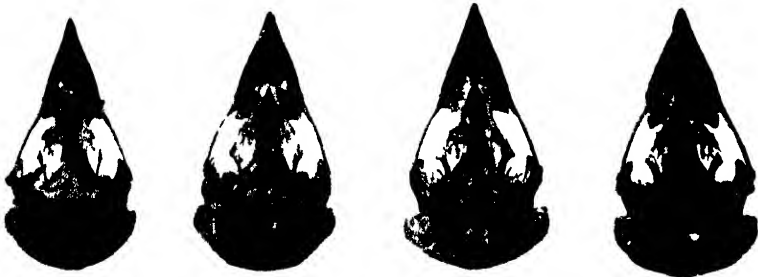
*b*



*c*

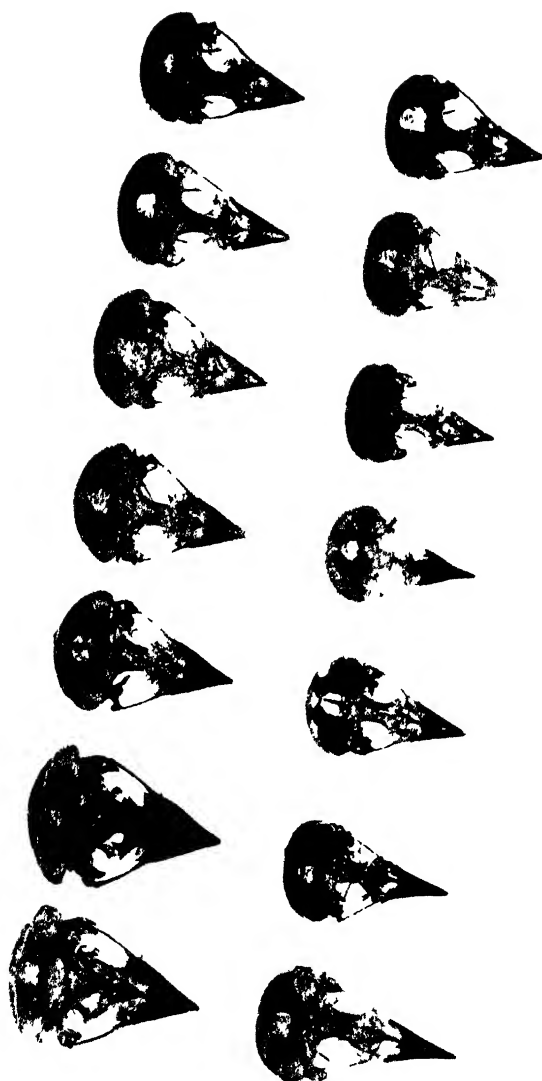


*d*



## PLATE 20

Ventral views of skulls of which measurements are given in table 25. In row *a* from top to bottom are skulls of these races of fox sparrows: *schistacea*, *fuliginosa*, *iliaca*, *sinuosa*, *unalascensis*, *brevicauda*, and *stephensi*. In row *b* from top to bottom are skulls of these song sparrows (except the fourth skull from the top): *fisherella*, *melodia*, *pusillula*, *lincolnii* *lincolnii*, *mailliardi*, *rufina*, and *sanaka*.



*a*

*b*



THE MOLTS OF THE LOGGERHEAD SHRIKE  
LANIUS LUDOVICIANUS LINNAEUS

BY

ALDEN H. MILLER

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 13, pp. 393-417, 4 figures in text

Issued November 8, 1928

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# THE MOLTS OF THE LOGGERHEAD SHRIKE *LANIUS LUDOVICIANUS* LINNAEUS

BY

ALDEN H. MILLER

(Contribution from the University of California Museum of Vertebrate Zoology)

---

## INTRODUCTION

Having recently undertaken an analysis of the taxonomy of the North American shrikes, I have been forced to realize the necessity for an understanding of all sex, age, and individual variation in plumage. This realization has led to the present study of molt, which it is hoped will make for more accurate indentifications and descriptions of the subspecies of *Lanius ludovicianus*. Only the molts subsequent to the juvenal plumage will be given consideration. No opportunity was presented to examine nestling birds and such a study, although of value, would be of less importance for our present needs. Besides, as Dwight (1905, p. 516) has pointed out, it is only after the juvenal stage that we commonly encounter the interesting admixtures of plumage, due to partial molts, that may characterize different groups and species.

The great similarity in natal and juvenal feathers among different species of birds is usually thought of as being due to a recapitulation of a former condition common among the adults. Accordingly, first fall, first prenuptial, second fall, and second prenuptial molts will be mentioned, together with descriptions of the juvenal plumage and of the alar pterylae, the knowledge of which is essential to this study. After the second fall molt, so far as can be ascertained at this time, the birds are fully adult, and no further modification of the winter or spring plumages occurs. Some statements by authors who touch on this subject will permit of clarification and elaboration. The writer will also attempt to harmonize this work with investigations made on other species and on molts in general.

Acknowledgment is made to Dr. Joseph Grinnell for his kindly suggestions and assistance during the course of this study.



## LITERATURE

Nitzsch (1867), in his publication on pterylography, did not discuss molt but did speak of the ten-primaried condition in *Lanius* as determined in European members of this genus. Coues (1876), who went into the question of primary number in Oscines rather more fully than Nitzsch, maintained that all of this sub-order have at least a rudimentary tenth primary, and suggested the possible existence of a rudimentary eleventh primary. The subject of primary number was again raised by Jeffries (1881), but, as with Coues, no mention was made of any careful examination of shrikes. At about this time Streets (1883) published an article on the immature plumage of North American shrikes. This article is a little misleading inasmuch as the author, having little material at hand and consequently incorrectly identifying the juvenal and immature plumages, contributed little to the knowledge of the subject, and made no real solution of the problem of shrike relationships, which solution is suggested by the title. A more extensive treatise on the phylogeny of *Lanius* and of the family Laniidae was that of Schiebel (1906), wherein suggestions were made pertaining to the relationships of the subspecies of *Lanius ludovicianus*. While he said little about molt or the plumage cycle, which is our present concern, nevertheless his interpretations of the vermiculations on adult and juvenal body plumage showed that he had correctly identified the feathers involved.

Gadow and Selenka (1893) gave a thorough treatise on pterylosis, and, although there have been many subsequent special studies of this subject, this work in Bronn's *Thierreich* still stands as a useful general reference on pterylosis. The discussion of molt is general and brief, but the authors established the principles of feather loss, growth, and order of replacement.

Turning to articles dealing specifically with *Lanius ludovicianus* we find Witmer Stone (1896) giving the first account of shrike molt. The nature of the mixed plumage of the first-year bird was merely suggested, since no complete investigation was undertaken. William Palmer (1898) furnished the most complete analysis of shrike molt so far published. From this work I have gained many suggestions and, indeed, in a number of instances I have been able merely to prove statements which he, through lack of material, was able only to advance as probabilities. He discussed the progression of the molt

in the adult and the immature, and noted the prenuptial feather replacements. Slightly later, Dwight (1900) summarized the molts of the shrike in concise manner, but uncovered few facts not mentioned by Palmer. The general principles of passerine molt set forth by Dwight are useful, but the student of today is impressed with the difficulty of making laws to govern the molts of all birds of any large systematic group. Molt cycles often separately characterize species within the genus; so it becomes dangerous to say a whole order of birds behaves in any particular way until all member species have been thoroughly studied.

More recently several articles have appeared that contribute to the knowledge of wing feathering. Reichling (1915) returned to the subject of primaries in Oscines, besides describing the wings of many other groups of birds. He followed Gadow and Selenka in his interpretations and designations of primaries and coverts. Papers by W. DeW. Miller (1915 and 1924) contributed further to the knowledge of wing pterylosis and established the wing formulas of many of our New World species. His nomenclature is different from that of Reichling, and some of the apparent disagreement on the part of these two authors as to the presence of certain feathers in the wing is in part due to this fact. However, by far the most complete and authoritative work on wing feathers is that of Steiner (1918). His investigations and explanations of diastotaxy involved the entire fore limb and provide a reliable basis for future research in this field.

## MATERIALS AND METHODS

The collection at the California Museum of Vertebrate Zoology contains 331 Loggerhead Shrikes (*Lanius ludovicianus*) which were available for study. Loaned specimens from the private collections of G. Frean Morcom, John R. Pemberton, Harry S. Swarth, and Loye Miller, together with the few I have collected myself, bring the total number of birds to 377. Most of these specimens come from California and adjacent parts of Oregon, Nevada, Arizona, and Lower California. The bulk of the material is therefore at present classed under the subspecies *gambeli* and *excubitorides*. There are two *mearnsi* from San Clemente Island, four *anthonyi* from Santa Cruz and Santa Catalina Islands, and a small series of *grinnelli* and *nelsoni* from Lower California. Seven of the subspecies *ludovicianus* from Florida, and three *migrans* from the Great Lakes region com-

plete the number. Birds in all stages of molt are present in the series of western skins, and there are sufficient specimens from other regions, I believe, to make the findings generally applicable to the entire species *Lanius ludovicianus*, with certain exceptions to be noted later.

Three California Shrikes preserved in alcohol afforded means for dissection of the wing and the study of pterylosis. Drawings were made of the wing to serve as a guide for a more accurate and rapid designation of the molting birds than would be possible from a study of dried materials only. In addition to fifty detailed descriptions of significant molting individuals, made on the basis of these drawings, the plumage of each bird available was appraised. The experience gained in recognizing differential wearing of feathers and fading of pigments proved valuable in the study of worn spring and summer plumages. Lastly it seemed advisable to compile in tabular form the occurrence of juvenal secondaries in the first-year shrikes, and to illustrate in similar manner the dates and sequence of feather replacements.

#### PTERYLOGRAPHY OF THE WING

The remiges, consisting of primaries and secondaries, are nineteen in number. The three proximal secondaries were termed tertiaries by Dwight (1900, p. 89) even though he stated that they are located on the ulna. The fact that the three proximal feathers seemed to molt apart from the remaining six distal secondaries, led him to adopt this separate terminology. In shrikes, as will be shown later, this distinction does not hold, and it therefore seems advisable to restrict the term tertiaries, as has been customary, to the flight feathers along the posterior edge of the humerus. The true tertiaries in *Lanius ludovicianus* form an indefinite series of about six feathers of from 10 to 18 millimeters in length, which are hardly to be distinguished from the adjacent upper coverts of the humerus. Reichling (1915, p. 239) termed all feathers on the upper surface of the humerus, which are usually concealed under the scapulars, *Tectrices humerales superiores*, so classing them as coverts but explaining that at times some may take on the form of cubital remiges. Judging from the form and location of these feathers in shrikes, Reichling's conception is probably correct. The nine secondaries are of eutaxic arrangement and the greater coverts of the secondaries are accordingly "regular." The most proximal secondary, number nine, is small and approaches the size of the greater upper coverts (see fig. 2).

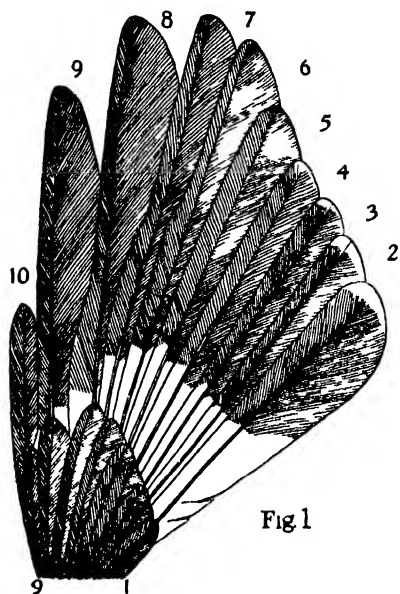


Fig 1

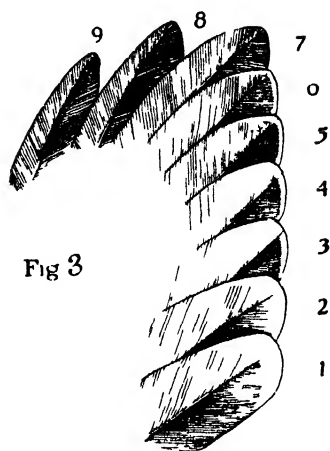


Fig 3

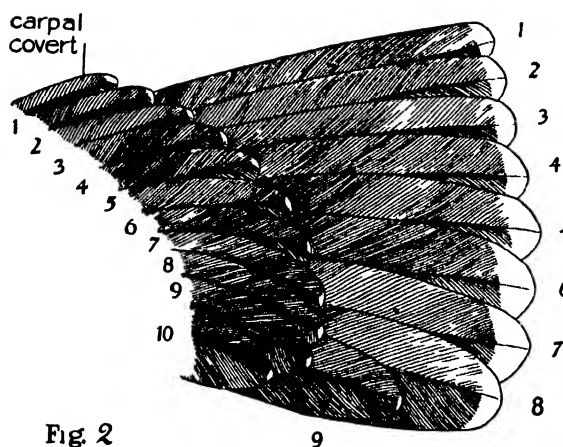


Fig 2

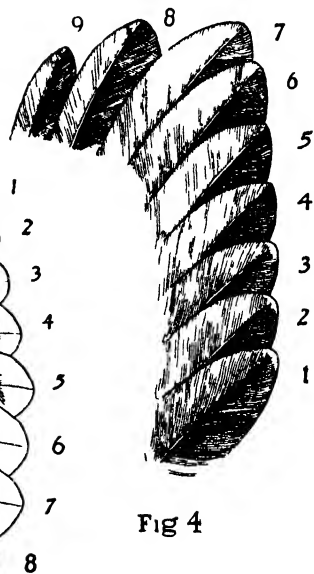


Fig 4

Figs 1-4 Dorsal views of the right wing of *Lanius ludovicianus gambeli*. Fig. 1, primaries and greater primary upper coverts,  $\times 1$ , male, adult, no 36943, Pasadena, California, December 23, 1899. The tenth covert is not shown. Fig 2, secondaries, greater secondary upper coverts, and carpal covert of the same specimen,  $\times 1$ . Fig 3, juvenile, greater primary upper coverts,  $\times 2$ , male, first year, no 30069, San Lucas, Monterey County, California, November 27, 1918. Fig 4, adult greater primary upper coverts,  $\times 2$ , female, adult, no 25200, Snelling, Merced County, California, January 7, 1915.

Of the ten primaries, which are all readily distinguishable superficially from the secondaries by a basal white area extending across both webs, the first six are bound on to the fused metacarpals. Primary seven is on the phalanx of digit three, and eight and nine on the proximal phalanx of digit two, so far as known the universal condition in passerines. The sixth, seventh, and eighth primaries form the tip of the wing, with either the seventh or eighth the longest. The well developed tenth primary is on the distal phalanx of digit two. On the dorsolateral surface of this phalanx there is a small white feather 5.5 millimeters long obscured by the white (tenth) greater upper covert which is 6.5 millimeters long. The insertion and shape of the former feather strongly suggests its homology with an eleventh primary, and tends to support the statements of Miller (1924) and Gadow and Selenka (1893) relative to the occurrence of vestigial primary remiges.

Each of the ten greater upper coverts of the ulnar region, except the most proximal member of the series, is inserted dorsally and proximally to a secondary, but immediately crosses over the calamus of its remex to the distal side. The exception, covert number ten, has no corresponding secondary and lies immediately proximal to covert number nine. Evidence brought forth by Steiner (1918, p. 224) shows that all greater upper coverts in the embryo lie distal to the remiges, and that on the forearm, during later development, the points of insertion shift to the proximal sides of the secondaries. Accordingly, the coverts of the hand region lie between and distal to the corresponding primaries, contrary to the statements of Gadow (1893, p. 557) and Reichling (1915, p. 307). This confusion in the nomenclature of the coverts accounts for the differing statements made by Miller as opposed to Reichling and Gadow regarding the reduction of first and second greater primary coverts. In Loggerhead Shrikes there is a covert, proximal to primary one, that is 9.0 millimeters shorter than the following true first primary covert, and similar in shape, color of tip, and mode of insertion to the coverts found on the secondaries (fig. 2). According to Steiner (1918, p. 422) this feather, which is similar in other passerines, is the carpal covert, now associated with the first primary but originally associated with a carpal remex that has been lost.

The much smaller middle coverts of the forearm lie distal to and between, thus alternating with, the greater coverts. There is no middle covert proximal to the greater ulnar covert, number ten. On

the hand the much reduced middle coverts are likewise distal to the greater coverts. The first three members of the series are either lacking or extremely small, and distally the middle coverts merge with the marginal feathers. The alula, consisting of three principal feathers of which the outermost is the greatest, obscures the middle coverts of the hand. Separated for the most part from the middle and humeral coverts by an apterium, several irregular rows of marginal feathers follow to complete the upper covering of the wing.

The undersurface of the wing bears two complete rows of coverts near the bases of the primaries. The insertions and locations of these greater and middle under coverts are not so definite nor so constant throughout the series as in the case of the upper coverts. In general, each greater covert is situated between two primaries. The middle coverts in the hand region lie anterior and slightly proximal to the greater coverts. They are anterior and distal to the greater coverts along the forearm. The marginal feathers on the under surface are continuous with the upper marginal coverts.

#### JUVENAL PLUMAGE

*Above:* Forehead, crown, hind neck, and nape smoke gray, each feather with one dusky bar 0.5 mm. wide, 1.0 mm. from the tip; back light grayish olive, each feather with smoke gray tip and dusky bar 0.5 mm. wide; rump and upper tail coverts smoke gray, each feather with subterminal dusky bar and two additional bars at 2 mm. intervals; rictal bristles and bristle-like tips of loreal feathers black; lores otherwise gray; auricular, antorbital, and suborbital regions deep blackish brown or dull black.

*Below:* Chin and throat white; breast and flanks smoke gray, each feather with two dusky bars 2.0 mm. apart; belly and under tail coverts white, with subterminal dusky bars on median coverts in some individuals.

*Wing:* Primaries deep blackish brown with both webs white basally, but with the white more extensive and more abruptly defined on the outer web; in general, the brown and white less clearly separated than in the adult, and the white spots of nearly equal size on primaries 5, 6, and 7 (see fig. 1); primary 5 slightly tipped with light buff, primaries 4, 3, 2, and 1 with progressively broader light buff tips, reaching a maximum width of 2.2 mm.; proximal portions of inner primary webs adjoining the basal white spots, fading to smoke gray; secondaries deep blackish brown fading basally to smoke gray; tips light buff similar to those of proximal primaries, but gradually

increasing in width to 3.0 mm. on secondaries 6, 7, 8, and 9, and becoming more nearly cinnamon buff; border between buff and brown on innermost secondaries usually irregular, and on secondaries 8 and 9 small cinnamon spots often appearing near, but separate from, the tip; greater primary upper coverts blackish brown, each completely tipped with a light buff area 1.0 mm. wide; greater secondary upper coverts with clay colored tips 1.5 mm. wide, and clay colored median subterminal spots or bars; all middle upper coverts and marginals similarly tipped and barred with cinnamon buff; feathers of alula bordered with light buff; under marginals and axillars white; greater and middle under coverts gray with dusky margins; lateral scapulars dull white, each with a dusky bar 2.0 mm. from tip followed by a less distinct bar 3.0 mm. proximally from the former; the more median scapulars, and bases of lateral scapulars, light grayish olive.

*Tail:* Four middle rectrices black, with 2.0 mm. margins of cinnamon buff and often a subterminal median buff spot separate from tip; eight remaining rectrices black, extensively but irregularly tipped with light buff or white, rarely having median buff spots; outer webs of outermost rectrices edged with white or buff from tips to bases—extent, shape, and definition of light areas subject to variation as in the adult.

*Bill and feet:* Both, when dry, various shades of brown, but not black as in the adult.

As far as possible the colors mentioned above are based on Ridgway's Color Standards (1912). The width of the feather margins, disregarding wear, is variable and the measurements are employed merely to describe the average condition. The description is based on juvenal specimens from the San Joaquin Valley of California, and therefore applies to *gambeli*. There are differences among the juvenal plumages of the various subspecies, but the characters listed above are applicable for the most part to all of the western representatives of *Lanius ludovicianus*. The vermiculations of the juvenile are much subject to change due to wear, but may be identified as juvenal by inspection of the individual feather pattern.

In the adult, in contrast to the juvenile, vermiculations are either lacking or are of a distinctly different type. The blackish brown parts of the juvenile are changed to black. The buff of the juvenal remiges, rectrices, and feathers of the alula is replaced by white, and there are no subterminal bars or spots on these feathers. The white tips of the fifth, sixth and seventh secondaries are usually wider than 3.0 millimeters, but the tip of the eighth is only half as wide, and that of the ninth reduced to a median terminal dot. The edging of

the two median rectrices is also reduced to a median dot and the borders between all light and dark areas are more definite. All greater and middle upper coverts are black with faint white terminal dots. In harmony with the color of the mantle, the upper marginal feathers are either gray tipped or entirely gray. The lateral scapulars are pure white. These comparisons have proved to be the most reliable criteria for distinguishing the individual juvenal and adult feathers.

#### ABRASION, DISINTEGRATION, AND ADVENTITIOUS COLORATION

The light-colored areas of all the feathers are more subject to abrasion than the brown and the black areas. In spring and early summer specimens, the light tips of the remiges and rectrices are invariably reduced in size and often completely worn off, in which case the shape of the feather tip conforms closely with the original line between black and light. Feathers, for example the juvenal greater upper primary coverts, that may have lost their tipping, can still be recognized with reasonable certainty by this means. The light tips of vermiculated feathers are quickly lost. Abrasion is more rapid in all juvenal feathers than in those of the adult, due no doubt to the more lax character of the vane. As in most birds, shrikes, after the breeding season, may possess many contour feathers that have been worn bare of the barbules or even of a large portion of the barbs.

Disintegration of certain of the cornified cell layers of the feathers is presumably the cause of the fading of the black pigments which they contain to various shades of brown. Juvenal remiges seem to fade more than do the remiges of adults, but this is a doubtful difference, and is due in part to the fact that some juvenal remiges are carried for longer than one year and thus may be actually older than the adult feathers with which they are commonly compared. Furthermore it must be remembered that, to start with, fresh juvenal remiges are blackish brown rather than black.

Adventitious coloration seriously obscures the observation of any possible fading of colors other than those just mentioned. The light-colored and comparatively soft body plumage of the species is readily soiled, and the whites and slate-grays are soon turned to buffs and browns. The degree of soiling is enhanced by the habit, prevalent among the birds in some parts of the country, of perching along the wires that follow the steam railways.



## FIRST FALL MOLT

The first fall molt of *Lanius ludovicianus* is always a partial molt resulting in the more or less mixed plumage of the first-year bird, which is not materially changed until the following summer. The order of the feather loss and replacement at this postjuvenile molt is subject to considerable variation as is apparent when a large number of molting specimens is examined. However, there is a recognizable order, followed by the majority of individuals, which is worthy of note. The exacting process of molting, it may be assumed, is naturally hindered or controlled by the general physiological condition of the bird, which in turn is particularly unstable in individuals that are first experiencing the severe environmental factors shortly succeeding the annual increase in population. More than in the adult, then, we find cases of retarded and interrupted molts.

The marginal coverts of the wing are the first feathers of the entire plumage to start molting. The replacement is gradual, beginning at a point on the extreme margin near the middle of the forearm, and progressing proximally, distally, and posteriorly through the irregular rows of marginals of both surfaces of the wing. This change consumes considerable time, and is not yet complete when, on an average of about a month later, the succeeding stages of the molt are initiated. The body molt starts on the back between the shoulders, and on the breast, thence progressing gradually forward and backward in the feather tracts concerned, toward the head and tail. At the inception of the body molt, or slightly later, the middle upper coverts of the arm drop, either as a series or in irregular progression from the elbow distally. Nearly all of this series is replaced before the greater secondary upper coverts drop. In the latter feathers, activity starts at the elbow and wrist and progresses rapidly toward the center of the forearm. However, the order within the series, both of middle and greater upper coverts of the arm, is particularly subject to variation. As the greater secondary upper coverts are growing in, the middle coverts and the distal marginals of the hand are being replaced.

During the change of the wing coverts, the body molt extends to the head, and to the coverts of the tail. Following this, part or all of the rectrices may molt, the replacement usually progressing from the central pair outward. In some specimens the molt has been observed to start from both margins and the center of the tail simul-

taneously. If the outer primaries molt, the process takes place during the same period in which the tail is being replaced, although more time is usually required to complete the molt of the primaries than is required for the molt of the rectrices. The primary molt starts with the fifth, sixth, or seventh primary feather and progresses outward. As in most progressive molts of the remiges, there is rarely more than one feather completely lacking at any given time. The alula changes during the replacement of the digital primaries. Slightly after the beginning of the replacement of the rectrices, or at a corresponding period in the event that the juvenal tail is retained, the scapulars and the proximal secondaries start to molt. The eighth secondary is dropped first, and as the new feather is growing, numbers nine and seven are lost. Replacement of numbers six, five, and four, if such replacement occurs, proceeds in the order given.

The greater primary upper coverts, and some proximal primaries and distal secondaries are not molted. Unfortunately the axillars, humeral feathers, and under wing coverts could not be studied to good effect in the dry skins, thus eliminating the possibility of detecting any correlation between the activity of the reversed under coverts and the other major feathers of the wing. The distal greater under coverts have been seen to molt with the distal primaries, yet in other specimens the primary molt is apparently unaccompanied by any change in the under coverts.

Through a comparison of dates taken from a large number of molting birds a general conception of the relative time and duration of each stage of the molt is gained. This supplements the above description which has been compiled after an inspection of a progressive series of molting juveniles, and gives a more complete picture of the entire process. Skins of *gambeli* have offered the best material for comparison, both in point of number and because of the fact that the dates in this group happen to be distributed evenly over the period from May to November. In the following table the total extent of each period is indicated by the two extreme dates upon which the particular condition is encountered, and the average or peak of each period is derived by calculating the mean date for all birds falling within the group. Only the major divisions of the process could be tabulated successfully by this method.

The great amount of time consumed in the molt involving the marginal and middle upper coverts is illustrated in the table. The more rapid change of the greater secondary upper coverts is indicated

by the small number of skins which show this stage, and by the relatively short total extent of the period. Although the body and middle covert molts start at nearly the same time in any given individual, the body molt requires more time for completion, thus placing the mean for this period later. As would be expected, the dates of the tail and primary replacement correspond closely. The inner secondary molt occurs distinctly later than the primary molt, and on the average marks the completion of the entire process, especially in individuals in which a large number of secondaries are changed.

TABLE 1  
PERIODS OF THE FIRST FALL MOLT  
*Lanius ludovicianus gambeli*

| Period of molt                                | Number of specimens | Total extent     | Mean     |
|---|---------------------|------------------|----------|
| No molt yet in evidence                       | 9                   | Up to June 23    |          |
| Marginal coverts only                         | 22                  | Apr. 24-Aug. 8   | June 20  |
| Upper middle coverts, but not greater coverts | 19                  | June 19-Sept. 21 | Aug. 2   |
| Body  | 25                  | July 17-Oct. 3   | Aug. 26  |
| Upper greater secondary coverts               | 5                   | Aug. 8-Sept. 22  | Sept. 2  |
| Tail  | 16                  | Sept. 6-Oct. 14  | Sept. 14 |
| Primary ...                                   | 12                  | Sept. 6-Oct. 14  | Sept. 16 |
| Inner secondary                               | 13                  | Sept. 6-Nov. 27  | Oct. 3   |

Much of the variation in the actual dates of molt is due to difference of locality. Furthermore, the figures are somewhat influenced by the collection of several individuals on the same day and at the same place. Birds from the same locality are probably often from the same brood, and as a rule such show great similarity in advancement of feather replacements. It is probable that the date of hatching affects the date of the molt as well as the degree of mixture of the first-year plumage. Nevertheless, the order of the process is fairly well established and it seems certain that in this subspecies the molt extends over a period of three and one-half months, from June 20 to October 3, though, as shown in the table, molting may be expected any time between the last of April and the first of December.

In *excubitorides* the specimens have been obtained from more diverse localities than in the case of *gambeli*, and there are unfortunate breaks in the molt series which render the comparison of dates in this subspecies less conclusive. However, the same general molt order is seen. Again, the molt lasts three and one-half months, but

in this case from July 10 to October 20; in other words, it is about twenty days later than in *gambeli*. Molting individuals may be found between the last of May and the first week of November. It would appear that the whole process in *excubitorides* is less variable as to date, regardless of a great diversity of localities. We may, perhaps tentatively, ascribe this difference to a sharper definition of the seasons in the regions distant from the coast that typify the habitat of *excubitorides*. The milder winters of the coastal slope of California would make possible early breeding and late completion of the molt, as obtaining in *gambeli*.

TABLE 2  
PERIODS OF THE FIRST FALL MOLT  
*Lanius ludovicianus excubitorides*

| Period of molt                                | Number of specimens | Total extent    | Mean     |
|---|---------------------|-----------------|----------|
| No molt yet in evidence                       | 11                  | Up to July 3    |          |
| Marginal coverts only                         | 12                  | May 31-Sept. 5  | July 10  |
| Upper middle coverts, but not greater coverts | 30                  | June 25-Sept. 8 | Aug. 12  |
| Body  | 24                  | July 13-Sept. 8 | Aug. 19  |
| Upper greater secondary coverts               | 3*                  | Aug. 2-Aug. 31  | Aug. 19  |
| Tail  | 5                   | July 16-Oct. 17 | Sept. 25 |
| Primary                                       | 3*                  | Oct. 9-Oct. 15  | Oct. 13  |
| Inner secondary                               | 7                   | Oct. 5-Nov. 5   | Oct. 20  |

\* Insignificant, because of small number of specimens.

A group of seven *excubitorides*, from an elevation of 6000 feet in the San Francisco Mountain region of Arizona, was not included in table 2. These birds are decidedly later in the molt. The mean of the period for the middle coverts is September 29, and the body molt averages about the same.

In eight *grinnelli* from Lower California the average date for middle covert and body molt is March 27. One individual, however, shows secondary and tail molt on October 30. The only *nelsoni* in early molt is a bird of May 30 showing activity in the marginals only. Another *nelsoni* is in primary and tail molt on October 9. Indications are that the process is much more extended in these two races from Lower California. Were more material available valuable comparisons of the effect of conditions in the subtropics on the molt within this group might be made.

The following descriptions have been chosen from the considerable number recorded in the author's manuscript notes, for the purpose

of illustrating in detail the course of the first fall molt. All numbers of specimens referred to in this paper are those of the California Museum of Vertebrate Zoology unless otherwise noted.

No. 3674; *gambeli* ♂; June 1. First two anterior rows of dorsal arm marginals new; all other feathers juvenal.

No. 36943; *gambeli* ♀; June 19. All arm marginals new; hand and part of wrist juvenal; the three innermost, middle arm upper coverts new, one covert lacking, and others juvenal; a few breast feathers new; all else juvenal.

No. 31135; *gambeli* ♀; July 17. All marginals new, except distally on hand; the four innermost, middle arm coverts new, others old; belly, throat, neck, and crown in height of molt; breast and center of back mostly new; tail coverts and all other parts juvenal.

No. 28574; *excubitorides* ♂; September 3. All marginals new, except distally on hand; middle arm coverts all new; middle hand coverts still juvenal; back, breast, and belly mostly new; forehead, throat, and rump in height of molt; tail coverts and all other parts juvenal.

No. 20647; *gambeli* ♀; August 3. All marginals apparently new; middle arm coverts new; middle hand coverts in process of growth; back, breast, belly, throat, and crown mostly new; tail coverts and rump partly juvenal; rectrices 1-1 (central pair) growing in, others juvenal; remiges, greater primary coverts, alula, and scapulars juvenal.

No. 36926; *gambeli* ♂; September 22. Extreme distal marginals still molting; middle arm coverts new, except for one feather; middle hand coverts nearly all new, greater secondary coverts 9 and 10 nearly full grown, others out; back, breast, rump, and belly mostly new; tail coverts, crown, and throat part juvenal; rectrices 1-1 growing in, 2-2 out, others juvenal; remiges, greater primary coverts, alula, and scapulars juvenal.

No. 3379; *gambeli* ♀; September 23. Upper wing coverts, except greater primary coverts, new; body new, except crown; tail coverts new; rectrices 1-1 partly grown, 2-2 out, others juvenal; primary 6, one-fourth grown, all others juvenal; alula, scapulars, and secondaries juvenal.

No. 36955; *gambeli* ♂; September 22. Upper wing coverts, except greater primary coverts, new; body new, except crown and throat; tail coverts new; rectrices badly torn, but 1-1, 2-2 and 3-3, new; primary 6, seven-eighths grown, 7, one-half grown, all others juvenal; alula juvenal; secondary 8, three-fourths grown, others old; scapulars molting.

No. 11195; *gambeli* ♂; September 10. Upper wing coverts, except greater primary coverts, new; body new, except crown and chin; tail coverts new; rectrices 1-1 new, 2-2, two-thirds grown, 3-3, one-third grown, 4-4, 5-5 and 6-6 juvenal; primary 5 new, 6, seven-eighths grown, 7 starting, all others old; alula juvenal; secondary 8, one-half grown, others old; scapulars molting.

No. 31331; *gambeli* ♂; October 26. Upper wing coverts, except greater primary coverts, new; body and tail coverts entirely new;

rectrices all new, but 2-2 slightly short, and outer eight partly grown; primaries 6 and 7 new, 8, two-thirds grown, 9 just starting, 10 out, others juvenal; greater primary under coverts molting; alula partly grown; secondary 8 new, 9 out, 7 just starting; scapulars new.

No. 27458; *gambeli* ♀; October 11. Upper wing coverts, except greater primary coverts, new; body and tail coverts new; rectrices 1-1 and 2-2 new, others new but varyingly short; primaries 5 and 6 new, 7, seven-eighths grown, 8, two-thirds grown, 9 just starting, others juvenal; secondaries 8 and 9 new, 7 partly grown, others juvenal; alula growing in; scapulars partly new.

No. 27459; *gambeli* ♂; October 9. Upper wing coverts, except greater primary coverts, new; body, except extreme chin and forehead, new; rectrices new, three outer pairs slightly short; primaries 5, 6, and 7 new, 8, three-fourths grown, 9, one-third grown, 10 out, others juvenal; secondaries 8 and 9 new, 7 slightly short, others juvenal; alula new; scapulars mostly new.

#### FIRST WINTER PLUMAGE

The mixed plumage, the result of the first fall molt, is composed principally of new feathers. All attempts to differentiate the new first-year feathers from corresponding second year feathers have failed. In the light of present observations, the vermiculations, the black mask, the scapulars, feather tippings, rump, and new remiges and rectrices, as well as the general coloration of the body plumage, are on the average the same in first-year birds as in second-year birds, although there is yet the possibility that some character will be found satisfactorily to distinguish the ages of some of these feathers.

The retained juvenal feathers that mark the first-year bird are variable in number. The juvenal, buff-tipped, greater primary upper coverts almost without exception are all retained. In one first-year *gambeli*, no. 27457, numbers five, six, seven, and eight of this primary covert series are new, and number ten is missing. Two of the three available first-year *grinnelli* likewise have a partial replacement of this series. No other positive cases are known of juvenal primary coverts having been lost. The presence of at least some juvenal feathers in the series is perhaps the most reliable criterion for designating first-year birds. The inner members of the series, that through wear lose the juvenal tipping less rapidly than the outer members, are usually recognizable up until the time of the second fall molt.

All, or as few as two, juvenal secondaries may be retained. When only one juvenal secondary is replaced, it is almost invariably number eight. If two are replaced, they are either numbers seven and eight,

or eight and nine. Tables 3 and 4 show the number of secondaries replaced and the per cent of the birds that lose each of the various secondaries. The correlation of molt order with degree of replacement is to be noted. More extensive replacement tends to occur in *excubitorides*, and probably also in *grinnelli*, than in *gambeli*. Only birds that have finished the molt are included in tables 3 and 4.

TABLE 3  
NUMBER OF SECONDARIES REPLACED

| Number of secondaries replaced           | 0 | 1 | 2 | 3  | 4  | 5 | 6 | 7 |
|--|---|---|---|----|----|---|---|---|
| Number of specimens showing replacement: |   |   |   |    |    |   |   |   |
| <i>gambeli</i>                           | 2 | 3 | 6 | 30 | 13 | 7 | 1 |   |
| <i>excubitorides</i>                     | 1 | 2 | 2 | 14 | 15 | 2 | 2 |   |
| <i>grinnelli</i>                         |   |   |   |    | 1  |   |   | 2 |
| <i>nelsoni</i>                           |   |   |   | 1  | 2  | 1 |   |   |
| <i>ludovicianus</i>                      | 1 |   | 1 | 1  | 1  |   |   |   |
| <i>migrans</i>                           | 1 |   |   |    | 1  |   |   |   |
| <i>anthonyi</i> and <i>mearnsi</i>       |   |   |   | 1  | 1  |   |   |   |

TABLE 4  
PER CENT REPLACEMENT OF EACH SECONDARY

| Secondary number     | 1     | 2    | 3   | 4    | 5     | 6    | 7    | 8    | 9    | 0   |
|----------------------|-------|------|-----|------|-------|------|------|------|------|-----|
|                      | %     | %    | %   | %    | %     | %    | %    | %    | %    | %   |
| Entire species       | 8     | 17   | 0 0 | 34   | 13 8  | 43 4 | 86 0 | 95 6 | 88 6 | 4 3 |
| <i>gambeli</i>       | 0 0   | 0 0  | 0 0 | 1 5  | 12 6  | 31 6 | 84 1 | 98 2 | 90 4 | 3 1 |
| <i>excubitorides</i> | 0 0   | 0 0  | 0 0 | 5 7  | 11 5  | 57 8 | 89 4 | 97 3 | 86 8 | 2 8 |
| <i>grinnelli</i>     | (33 3 | 66 6 | 0 0 | 33 3 | 66 6) |      |      |      |      |     |

As to the juvenal primaries, either all are retained, or the distal feathers that form the tip of the wing are replaced. Accordingly, four, five, or six proximal juvenal primaries are, as a rule, present. Again, in the two *grinnelli* previously mentioned with regard to the primary coverts, there is a more extensive replacement than in other specimens. No. 50242 appears to have no juvenal primaries, and in no. 50243, only primaries one and two are juvenal. Primaries in many instances are difficult to classify as to age, but in birds taken before January, I believe a diagnosis can be made with fair degree of accuracy. On this basis 30 per cent of the first-year birds show no primary replacement.

A similar age classification of alula and tail in the same specimens in which the primaries were studied shows that only birds with changed outer primaries have new alulae. Likewise, no birds with all primaries juvenal show new alulae. Only birds with all primaries juvenal show juvenal rectrices. A partly, or completely, juvenal tail appears in about 20 per cent of the first-year birds. A December specimen, no. 6309, with secondaries, primaries, and rectrices all juvenal, has several old greater secondary upper coverts.

Many first-year birds show brown on the beak, especially at the base of the lower mandible, but in others of the same age the beak is black.

These conditions, then, are the salient features of the first-year plumage.

#### PRENUPTIAL MOLTS

The prenuptial molts of first-year and of fully adult birds are similar in all respects, so far as can be ascertained from a study of the twenty-four specimens that exhibit any trace of this activity. As has been found to be the case in the annual molts, there is no sexual difference in the time or the extent of the process. The present observations on western Loggerhead Shrikes closely agree with Dwight's statement of the prenuptial molt of *Lanius ludovicianus* of New York State (Dwight, 1900, p. 235).

Although the annual body molt is completed, for the most part, in September and early October, growing feathers may be found on the throat even in November and December. This prolonged replacement has not been considered in the tabulation of the periods of the first fall molt because of its seemingly casual nature. Only during January are pinfeathers altogether wanting. From February to April, or rarely May, there is always a possibility of finding the throat and chin molting. The peak of activity occurs in the latter part of February and during March. Often the molt here involved is not apparent until the feathers are deranged, but in some birds it is sufficiently extensive to be obvious at first glance, and in these individuals there are often molts of the crown and forehead, as well as occasional new feathers on the breast and belly. Whether all birds undergo this molt and whether all individuals molt feathers other than those of the throat, could not be ascertained. At best, the prenuptial molts are little more than sporadic feather replacements, and the resulting freshening of the normally white throat produces little or no change in appearance.



## SECOND FALL MOLT

The order followed in this first complete molt differs in several respects from the order pursued during the first fall, but it is identical with subsequent annual molts. Because of this likeness, and the fact that birds of the second fall can be recognized as such only during the first half of any annual molt, shrikes of all ages, older than one year, have been used as a basis for the description of this process. Only nineteen specimens from both *gambeli* and *excubitorides* were available for this study, but they are well distributed throughout the different periods of the molt.

Primary number one and its greater upper covert are the first feathers dropped. Numbers two and three with their coverts follow, often before the new number one has reached one-fourth its full length. The remainder of the primaries and greater upper coverts are replaced more gradually, especially on the wing tip where the dropping of several primaries in quick succession would certainly materially affect the power of flight. The correlation between primaries and corresponding greater upper coverts is invariably close. Because of its comparative regularity and long duration, the primary replacement furnishes a convenient time scale for the other stages of the molt.

As the third primary is lost, the body molt starts, seemingly on the breast and back first, extending however to the head and rump far more rapidly than in the first fall molt. The tail coverts are dropped during the same period and often before the rump shows any pinfeathers. The median pair of rectrices drop at the same time as, or slightly after, the tail coverts. The marginal coverts at the center of the forearm start activity at the inception of the body molt.

The replacement of the greater secondary upper coverts usually starts with the dropping of the fourth primary and is rapidly completed, with only a slight tendency toward an ordered progression from either extremity of the forearm toward the center. Either secondary eight or one, or both, drop at this time. Numbers nine and seven follow, and number two is lost as number one is growing. The secondary replacement continues gradually toward the center of the arm, culminating with either number five or number six. Regardless of the fact that the secondary molt takes place at two points simultaneously, the last secondary is not fully grown until after the primaries are complete.

The middle upper coverts of the arm show irregular replacement, beginning with the loss of the fifth primary. Greater under coverts, and middle upper and under coverts of the hand molt slightly later, accompanied by the change of the hand marginals as in the first fall molt. The two median pairs of rectrices are well grown at this stage. As the tail molt progresses through the four lateral pairs of rectrices, the loss is more rapid, and it is not uncommon to find two or even three adjacent feathers just starting to grow at the same time. The tail becomes fully grown with the completion of the primary molt. The body plumage is apparently all new at the time of the seventh or eighth primary replacement, but scattered pinfeathers may be found much later, particularly on the throat, as before mentioned in connection with the prenuptial molts. The scapulars and alula molt with primaries eight and nine.

Because of the small number of specimens, the exact dates of the various stages of this molt could not be satisfactorily ascertained. In general, the first primaries are lost about the first of July. In the latter part of August, primaries five and six molt, and during September and the first week of October the primary series is completed. Some secondaries may still be short of normal length even in late October.

In lieu of a tabulation of the dates of molting, the accompanying graph serves to indicate the average time and sequence within annual molts after the first year.

TABLE 5  
SEQUENCE WITHIN ANNUAL MOLTS AFTER THE FIRST YEAR

| Date                                  | → July 1 |   |   |   | September 1 |   |   |   | October 1 |    |
|---------------------------------------|----------|---|---|---|-------------|---|---|---|-----------|----|
| Loss of primary no.                   | → 1      | 2 | 3 | 4 | 5           | 6 | 7 | 8 | 9         | 10 |
| <b>Molt Period</b>                    |          |   |   |   |             |   |   |   |           |    |
| Primaries                             |          |   |   |   |             |   |   |   |           |    |
| Greater primary coverts               |          |   |   |   |             |   |   |   |           |    |
| Body                                  |          |   |   |   |             |   |   |   |           |    |
| Marginals of arm                      |          |   |   |   |             |   |   |   |           |    |
| Tail coverts                          |          |   |   |   |             |   |   |   |           |    |
| Rectrices                             |          |   |   |   |             |   |   |   |           |    |
| Greater secondary coverts             |          |   |   |   |             |   |   |   |           |    |
| Secondaries                           |          |   |   |   |             |   |   |   |           |    |
| Middle arm coverts                    |          |   |   |   |             |   |   |   |           |    |
| Middle and marginal hand<br>[coverts] |          |   |   |   |             |   |   |   |           |    |
| Alula                                 |          |   |   |   |             |   |   |   |           |    |

The following descriptions illustrate annual molts subsequent to the first year.

No. 40980; *excubitorides* ♂; July 23; older than two years. Primaries 1-1 out; greater primary upper coverts 1-1, and 2-2 out; all other feathers old.

No. 28554; *excubitorides* ♂; June 26; older than two years. Primaries 1-1, and 2-2 out; greater primary upper coverts 1-1, and 2-2 out; all other feathers old.

No. 22916; *gambeli* ♀; July 18; older than two years. Primary 1, one-fourth grown, 2, one-sixth grown, 3 out; greater primary upper covert 1, one-half grown, 2 and 3 out; middle back, breast, throat, and chin molting; marginal coverts on middle forearm molting; tail coverts out; rectrices 1-1, one-tenth grown.

No. 40984; *excubitorides* ♂; July 29; one year old. Primary 1 new, 2, seven-eighths grown, 3 starting, 4 out; greater primary upper covert 1 and 2 new, 3 out, others juvenal; back, neck, breast, throat, and chin molting; tail coverts, but not rump, molting; rectrices 1-1; one-eighth grown; arm marginals molting; greater secondary upper coverts molting at either extremity of forearm.

No. 47787; *nelsoni* ♀; July 27; (age ?). Primaries 1 and 2 new, 3, two-thirds grown, 4 starting; greater primary upper coverts 1, 2, and 3 new, 4 partly grown; back, head, breast, throat, chin, and flanks molting; tail coverts out, and rectrices old; arm marginals molting; greater secondary upper coverts molting, beginning at wrist; secondary 8, two-thirds grown.

No. 28570; *excubitorides* ♀; August 28; (age ?). Primaries 1, 2, 3, and 4 new, 5, nine-tenths grown; greater primary upper coverts 1, 2, and 3 new, 4 and 5 out; body molt well advanced in all regions; tail coverts new; rectrices 1-1 new, 2-2, nine-tenths grown; arm marginals and greater secondary upper coverts new; middle arm upper coverts molting without order; secondaries 8 and 9 new.

No. 28580; *excubitorides* ♂; September 6; one year old. Primaries 1 to 5 inclusive, new, 6, two-thirds grown; greater primary upper coverts 1 to 5 inclusive, new, 6 growing in; head, rump, breast, throat, belly and flanks still molting, but mostly new; tail coverts new; rectrices shot out, but 1-1, and 2-2 new, and 3-3 partly grown; arm marginals and greater secondary upper coverts new; middle arm upper coverts nearly all new; middle hand upper coverts and hand marginals molting; secondaries 8 and 1 new, 9, three-fifths grown, and 2 starting.

No. 30075; *gambeli* ♀; September 26; (age ?). Primaries 1 to 6 inclusive, new, 7, one-eighth grown; greater primary upper coverts 1 to 6 inclusive, new, 7 partly grown; back, rump, head, throat, and chin finishing molt; tail coverts new; rectrices 1-1 and 2-2 new, 3-3 starting; upper arm coverts all new; middle hand upper coverts and marginals molting; under hand coverts molting; alula old; secondaries 1, 2, 7, 8, and 9 new, 3 out.

No. 28583; *excubitorides* ♂; September 22; (age ?). Primaries 1 to 6 inclusive, new, 7, nine-tenths grown, 8, one-half grown, 9 starting, 10 out; greater primary upper coverts 1 to 8 inclusive, new, 9 partly grown; chin and crown molting, with scattered pinfeathers on other parts of body; rectrices 1-1, 2-2, and 3-3 new, 4-4, and 5-5, three-fourths grown, 6-6, one-sixth grown; all other wing coverts new; alula in process of growth; scapulars partly new; secondaries 1, 2, 3, 8, and 9 new, 4 starting, 7, three-fifths grown.

No. 36937; *gambeli* ♀; September 19; (age ?). Primaries 1 to 8 inclusive, new, 9, two-fifths grown, 10 old; greater primary upper coverts 1 to 9 inclusive, new; forehead, chin, and flanks still with a few pinfeathers; tail all new; all wing coverts new; scapulars mostly new; alula starting; secondaries 1, 2, 3, 6, 7, 8, and 9 new, 4, two-thirds grown, 5 old.

No. 3415; *gambeli* ♂; October 5; (age ?). Primaries 1 to 8 inclusive, new, 9, one-half grown, 10 starting; all wing coverts new; chin with a few pinfeathers; rectrices 5-5, and 6-6 a little short; scapulars new; alula nearly complete; secondaries 1, 2, 3, 7, 8, and 9 new, 4, one-fourth grown, 6, seven-eighths grown, 5 old.

No. 713, coll. H. S. Swarth; *gambeli* ♂; October 28; (age ?). Chin with a few pinfeathers; secondary 6 of one wing seven-eighths grown; remainder of plumage new.

## CONCLUSION

In review, and comparing the various molts, several points require special mention. The period of July, August, and September, during which adult annual molts have been found to occur, is probably a longer period than that required by any one average individual. The previously established mean period of three and one-half months for the incomplete molt of first fall birds seems to be at least fifteen or twenty days longer than the probable mean period for adults. In contrast with juvenal birds, adults show more rapid replacement within the different feather groups, as illustrated in the cases of the greater secondary coverts and the body plumage proper. The inceptions of the molts of the body, tail, wing coverts, and secondaries occur in rapid succession in the adult. From these and other considerations, adult molts may be characterized as more vigorous, precise, and rapid than the first fall molt. In adult molts the primaries initiate the entire process and the marginals fail to precede the body molt, whereas in first fall birds the process starts with the marginals, the other wing feathers and body plumage not changing until much later. It is perhaps significant that when the outer pri-

maries do molt in the first fall birds, the entire molt has reached a stage which corresponds with the stage in adults when the primary replacement has extended to the wing tip. Middle arm upper coverts follow the marginals, and the greater secondary upper coverts precede or start with the secondaries in both types of annual molt. However, the much earlier secondary molt in adults places the greater secondary covert molt before the middle arm covert replacement, the reverse of the condition found in the juvenile. Some adaptive significance would seem to be attached to this constant relation of secondaries and greater upper coverts, but the precise nature of this adaptation is not readily apparent.

Adult annual molts replace all feathers of the body. But, in first fall birds, only certain feathers being replaced, it would seem logical to suppose that these replacements constitute an adaptation for the purpose of reinforcing the most vulnerable parts of the plumage. Such plumage parts, although not seriously worn at the time of the first fall molt, might, if not replaced, reach a dangerous stage of disintegration by the following summer. In support of this suggestion, the outer primaries that form the wing tip, and the innermost secondaries that protect the outer secondaries and the dorsolateral body surface, have been seen to wear more rapidly than other remiges. Correspondingly, these more important feathers are commonly replaced during the first fall molt. The lax juvenal body plumage is always completely replaced. In partial tail molts, the long middle rectrices are replaced in preference to the lateral rectrices. In contrast to the replaced feathers, the strong, stiff, and for the most part well-protected greater primary upper coverts are retained. Likewise, the remiges protected in the angle of the wrist, which are also perhaps less essential for flying than the outer primaries, are practically never changed until after the first year.

Steiner (1918) in his treatise on diastataxy has established the fact that the rows of middle and greater upper and under coverts of the arm, and the secondaries, are each derived in the embryo from two separate series of feathers, one proximal and the other distal. The central point at which these series meet is subject to irregularities resulting in various eutaxic and diastataxic conditions peculiar to the region of the fifth secondary. In passerines the detailed developmental history of the mode of fusion of these complementary series is not well known. In full-grown individuals the rows of coverts and secondaries are regular throughout and give no certain indication of

double origin, like that found in certain other orders of birds. However, the double origin of the various series is reflected in the incompleteness of the feather replacements in first-year birds and in the order of molt. In the case of the feathers of the alula, the correspondence in time of molt with the digital primaries would seem to be a reflection of the phylogenetic relationship of these two groups of feathers. The alulae of shrikes, now serving perhaps chiefly as wing coverts, might be expected to molt with, or in definite relation to, the adjacent marginals, but such is not the case. Previous articles dealing with the adaptive significance of molt order have properly stressed the need of keeping the minimum level of plumage efficiency as high as possible. In the wings and tail this end is supposedly accomplished by the alternating molts of different series of feathers, and in the remiges and rectrices, particularly, by the replacement of the least important feathers first, in order that more of the series may be new when the most important feathers are lacking. In several instances this explanation is applicable. However, the fact that the long central pair of rectrices and the largest of the inner secondaries drop first and the fact that the alula and outer primaries are lacking at the same time are not easily explained on the same basis. The adaptations found in the degree of replacement in partial molts, and in certain features of molt order, seem obvious. But, although all phases of molt order must be adjusted at least to the extent that the birds are able readily to survive, I believe that there is still to be seen in the molt behavior of certain feathers, in addition to adaptation, a definite reflection of either embryonic, or phylogenetic homologies, and perhaps both.

### SUMMARY

In summary it may be noted that *Lanius ludovicianus* has been found by the present writer to correspond with other passerines in most details of wing pterylography. A number of distinctive features of the first fall molt are here described, and the variable condition of the first-year bird is analyzed. Some insight has been gained as to the adaptive features of the various molts, and evidence to substantiate Steiner's conclusions regarding the grouping of wing feathers has been presented. The prenuptial and adult annual molts are here described and compared. Variation of molt within the species and within the subspecies has been found and correlation with climatic differences suggested. Data have been compiled whereby juvenal

feathers may be readily detected, and the agencies of plumage alteration other than molt have been partially determined. This knowledge, coupled with the fact that no difference between new first-year feathers and adult feathers can be found, should aid in future taxonomic studies of this species, *Lanius ludovicianus*. Indications of subspecific divergence in molt behavior suggest that more extensive analyses of molts, undertaken either in this or in other species, would not only better establish principles of molt variation and adaptation but also might serve to determine to what extent such variations may be regarded as hereditary and therefore characteristic of the subspecies.

## LITERATURE CITED

- COUES, E.  
1876. On the number of primaries in Oscines. Bull. Nutt. Ornith. Club, 1, 60-63.
- DWIGHT, J., JR.  
1900. The sequence of plumages and moults of the Passerine birds of New York. Annals New York Acad. Sci., 13, no. 1, 73-360, 7 pls.  
1905. Sequence in moults and plumages, with an explanation of plumage cycles. Ornith., 14, 513-518.
- GADOW, H., and SELENKA, E.  
1891. Dr. H. G. Bronn's Klassen und Ordnungen des Thierreichs (C. F. Winter, Leipzig), 6, vierte Abtheilung, 2 systematischer Theil, 1-1008, 59 pls.
- JEFFRIES, J. A.  
1891. On the number of primaries in birds. Bull. Nutt. Ornith. Club, 6, 156-163.
- MILLER, W. DEW.  
1915. Notes on ptilosis with special reference to the feathering of the wing. Bull. Am. Mus. Nat. Hist., 34, 129-140.  
1924. Further notes on ptilosis. Bull. Am. Mus. Nat. Hist., 50, 305-331.
- NITZSCH, C. L.  
1867. Nitzsch's pterylography, translated from the German, edited by P. L. Selater (published for the Ray Society by Robt. Hardwicke, London), 1-181, 10 pls., 5 figs. in text.
- PALMER, W.  
1898. Our smaller eastern shrikes. Auk, 15, 244-258.
- REICHLING, H.  
1915. Die Flügelfedernkennzeichen der nordwestdeutschen Vögel. Jour. f. Ornithologie, 63, 229-267, 305-340, and 513-548, 7 pls.
- RIDGWAY, R.  
1912. Color standards and color nomenclature (published by the author, Washington, D. C.), 1-43, 53 pls.
- SCHIEBEL, G.  
1906. Die Phylogenie der *Lanius*-Arten. Jour. f. Ornithologie, 14, 1-77, and 161-219, 8 pls.
- STEINER, H.  
1918. Das Problem der Diastataxie des Vogelflügels. Zeitschrift f. Naturwissenschaft, 55, 221-496, 3 pls., 49 figs. in text.
- STONE, W.  
1896. The molting of birds with special reference to the plumages of the smaller land birds of eastern North America. Proc. Acad. Nat. Sci. Phila., 1896, 108-167, 2 pls.
- STREETS, T. H.  
1883. A study of the immature plumage of the North American shrikes to show their descent from a common progenitor. Am. Nat., 17, 389-390.





MAMMALS COLLECTED BY CHARLES D. BROWER  
AT POINT BARROW, ALASKA

BY

E. RAYMOND HALL.

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 14, pp. 419-425  
Issued March 19, 1929

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# MAMMALS COLLECTED BY CHARLES D. BROWER AT POINT BARROW, ALASKA

BY

E. RAYMOND HALL

(Contribution from the University of California Museum of Vertebrate Zoology)

---

In the winter of 1926-27, Mr. Charles D. Brower of Barrow, Alaska, visited the Museum of Vertebrate Zoology and, while looking over the collections therein, conceived the idea of sending to this museum specimens of birds and mammals which he believed would add to the meager information available about the fauna of northern Alaska. He has put this idea into effect, and to date, two shipments of specimens have been received from him. These comprise fifty-eight birds and ninety-seven mammals. Mr. Brower's industry will be appreciated by other students of natural history because the specimens, as recorded in the present paper, bring out several new facts regarding the mammals of northernmost Alaska. For instance, Mr. Brower's specimens extend the known ranges of three species, a shrew, a marmot, and a meadow mouse, several hundreds of miles. The native Eskimo names, precisely as written by Mr. Brower, are given here in parentheses after the English common names.

All catalogue numbers are those of the University of California Museum of Vertebrate Zoology and are inclusive. Unless otherwise stated, specimens are labeled as from Barrow, Alaska.

## ***Sorex tundrensis* Merriam**

### **Tundra Saddle-backed Shrew**

Nos. 39706 to 39718, taken from September 27 to October 11, 1927, inclusive. This occurrence extends the known range of the species about three hundred and twenty-five miles to the north. Bettles, near the head of the Koyukuk River, appears to be (see Jackson, 1928, p. 74) the locality nearest Barrow from which saddle-backed shrews previously have been reported. The species ranges entirely across Alaska, from the Seward Peninsula to the mouth of the Mackenzie

River. Thus the occurrence at Barrow makes it appear probable that the species occupies also all that part of Alaska north of the Arctic Circle.

Each of the specimens has assumed the winter coat. No. 39711 has the teeth but little worn and may represent a young adult. Each of the other specimens has the teeth worn to a degree that indicates the age to be adult.

Comparison of the skull measurements of the present series with measurements which Jackson (1928, p. 76) gives of ten specimens from more southern localities in Alaska indicates some geographic variation. The specimens from Barrow appear to have actually, as well as relatively, longer palates and upper tooth rows, although the condylobasal length for each of the eleven specimens from Barrow is less. The difference in inter-orbital breadth between the two series may be due to the use of a different technique in taking measurements.

TABLE 1

AVERAGE CRANIAL MEASUREMENTS (IN MILLIMETERS), WITH MINIMA AND MAXIMA IN PARENTHESES, OF *Sorex tundrensis* FROM ALASKA

The measurements of specimens from St. Michael and from near Eagle are taken from Jackson (1928, p. 76).

|                                     | LOCALITIES      |                               |
|-------------------------------------|-----------------|-------------------------------|
|                                     | Barrow          | St. Michael<br>and near Eagle |
| Number of individuals averaged..... | 13              | 10                            |
| Condylobasal length.....            | 17.7(17.2-17.9) | 18.1(17.8-18.5)               |
| Palatal length.....                 | 7.3(7.0-7.4)    | 7.0(6.7-7.2)                  |
| Cranial breadth.....                | 9.0(8.7-9.1)    | 9.1(9.0-9.3)                  |
| Interorbital breadth.....           | 3.5(3.3-3.8)    | 3.7(3.5-3.8)                  |
| Maxillary breadth.....              | 5.0(5.0-5.1)    | 5.0(4.8-5.1)                  |
| Maxillary tooth-row.....            | 6.5(6.3-6.6)    | 6.3(6.1-6.4)                  |

### ***Mustela arctica* (Merriam)**

Tundra Weasel (E-te-re-ah)

No. 40060, subadult male, taken in December, 1927. This topotype is in the white winter coat.

***Mustela rixosa eskimo* Stone**

Arctic Least Weasel (Now-la-you)

Three adult topotypes: no. 40057, adult male, in white winter pelage, taken in February, 1928; no. 40058, adult male, taken June 14, 1928, and no. 40059, adult female, taken June 15, 1928. Each of the latter two specimens is in the brown, fresh, summer coat.

***Vulpes fulva alascensis* Merriam**

Red Fox (Ky-ook-too; cross fox distinguished as Kairn-roe)

Nos. 40061 to 40071, skulls only, taken at Barrow, Alaska, in December, 1927, January and February, 1928. Male skulls exceed female skulls by about the same amount as in the case of *Alopex* from the same region. Combined individual and sex variations noted in the teeth are as follows: length of  $M_1$ , 17 per cent; length of  $P^4$  and  $M^1$ , 17 per cent; width of  $M^1$ , 20 per cent. By way of explanation, this means that the width of the narrowest (10.7 mm.)  $M^1$  is 20 per cent less than that of the widest (13.4 mm.)  $M^1$ .

***Alopex lagopus innuitus* (Merriam)**

Arctic Fox (Tir-ri gen-dia)

Nos. 40072 to 40097, taken in the winter months, December, 1927, to March, 1928, are virtual topotypes. The male skulls average slightly larger than the female skulls. In this connection Merriam (1902, p. 169) states that: "Among the Arctic foxes the difference [between male and female] in size of skull is usually not great, but the large upper molar, and the carnassial above and below are noticeably larger in the males." In the present series of skulls the width of  $M^1$  averages 4 per cent less in females and this difference is more than appears between the averages of the two sexes in any one of the other measurements taken. However, the present material does not bear out Merriam's statement about  $M^1$  and  $P^4$ . The combined length of these two teeth varies less than most other parts of the skull studied.

Individual variations noted in the teeth of the males are as follows: length of  $M_1$ , 19 per cent or one-fifth; length of  $P^4$  and  $M^1$ , 14 per cent; width of  $M^1$ , 17 per cent.

TABLE 2

AVERAGE, MAXIMUM, AND MINIMUM CRANIAL MEASUREMENTS (IN MILLIMETERS)  
OF NINE FEMALES AND SEVENTEEN MALES OF *Alopex lagopus innuitus*  
FROM BARROW, ALASKA

Among the males it happens that the maximum and minimum are throughout furnished by nos. 40094 and 40089, respectively.

|           | Length<br>of $M^1$ | Length<br>of<br>$P^1$ and $M^1$ | Width<br>of<br>$M^1$ | Basilar<br>length<br>(of Hensel) | Length<br>of<br>tooth rows | Zygomatic<br>breadth | Mastoid<br>breadth |
|-----------|--------------------|---------------------------------|----------------------|----------------------------------|----------------------------|----------------------|--------------------|
| Male      |                    |                                 |                      |                                  |                            |                      |                    |
| Average . | 13.9               | 19.6                            | 10.0                 | 111.7                            | 66.2                       | 67.9                 | 42.7               |
| Maximum   | 15.0               | 20.5                            | 10.9                 | 120.4                            | 72.0                       | 72.1                 | 46.3               |
| Minimum   | 12.2               | 17.7                            | 9.1                  | 105.9                            | 61.4                       | 63.7                 | 41.2               |
| Female    |                    |                                 |                      |                                  |                            |                      |                    |
| Average   | 13.7               | 19.4                            | 9.6                  | 107.8                            | 64.4                       | 65.6                 | 42.2               |
| Maximum   | 14.4               | 20.6                            | 10.6                 | 113.0                            | 67.3                       | 69.1                 | 43.6               |
| Minimum   | 12.9               | 18.4                            | 9.0                  | 103.7                            | 62.1                       | 62.7                 | 41.0               |

### ***Marmota caligata caligata* (Eschscholtz)**

#### Northern Hoary Marmot

No. 39719, a subadult, skull only, taken in August, 1927, at Cape Thompson, was brought to Mr. Brower by a native. The skull represents a subadult and, probably, partly on this account, is relatively slender for an individual of *Marmota caligata caligata*. Measurements of this skull are as follows: condylobasal length, 87.0; palatal length, 51.8; postpalatal length, 32.2; length of nasals, 34.8; zygomatic breadth, 55.2; breadth across mastoids, 38.1; least interorbital breadth, 22.0; breadth of rostrum, 18.9; maxillary tooth row, 21.1.

This specimen provides a large extension of range to the north and east. Cape Thompson is about two hundred and seventy miles from the nearest part of the mapped range (see Howell, 1915, p. 58) of *M. c. caligata* and more than five hundred and fifty miles from Fort Yukon, the locality nearest Cape Thompson from which Howell (*loc. cit.*, p. 61) records specimens. Although no specimens are known to the writer from north of Cape Thompson, hoary marmots evidently range farther north; for Bailey and Hendee (1926, p. 20) remark: "Marmots are fairly common throughout the hills of northern Alaska. The Eskimos told us they were numerous fifty miles inland from Wainwright."

**Citellus parryi kennicottii** (Ross)

Kennicott Ground Squirrel (Sic-ric)

Nos. 40098 and 40099, male adults, taken June 2, 1928, at Barrow, Alaska, and no. 39720, male, adult, taken September 29, 1927, on the Meade River, thirty miles from Barrow, Alaska. In reference to no. 39720, Mr. Brower writes that nearly all squirrels of this species had holed up by September 29, but that this individual took advantage of a warm spell of weather experienced in the region at this time, to have "a last look before going to sleep for the winter."

These specimens are topotypes of *Spermophilus barrowensis* Merriam (1900, p. 19) which Preble (1908, p. 162) regards as identical with *Citellus (Colobotis) parryi kennicotti*, first named by Ross (1861, p. 434) from near Fort Good Hope, Lower Mackenzie region, Mackenzie, Canada, as *A[rctomys]. kennicottii*.

In color, the specimens answer to Merriam's (*loc. cit.*) description except that the neck is gray rather than buffy in nos. 39720 and 40099.

The large size of this handsome spermophile is indicated by the following measurements, of no. 40099, taken from the dried skin: total length, 430; length of tail, 90; length of hind foot, 67. Pertinent skull measurements for no. 40099 and 39720, are, respectively, as follows: basilar length (of Hensel), 54.2, 52.0; occipitonasal length, 64.0, 63.0; zygomatic breadth, —, 41.5; length of nasals, 23.0, 21.9; alveolar length of molar and premolar teeth, 15.3, 15.2.

**Lemmus alascensis** Merriam

Point Barrow Lemming (Ah-vin ach)

Nos. 39721 to 39733, taken from September 5 to October 6, 1927, inclusive, and nos. 40100 to 40117, taken from November 19, 1927, to June 13, 1928, inclusive. This valuable series of thirty-one topotypes includes varying ages of each sex. The two largest individuals are nos. 40102 and 40117, adult males, whose large size is indicated, respectively, by the following cranial measurements: condylobasal length, 32.2, 32.6; length of nasals, 9.9, 8.7; greatest breadth of rostrum, 6.8, 7.1; zygomatic breadth, 22.1, 21.9; mastoid breadth, 16.9, 16.5.



The attached label of no. 40104, an adult female, bears the following interesting comment: "Found dead on ice, 6 mi. off shore, one [front] foot and tail partly gone and healed over, Dec. 16, 1927."

The color of the adult pelage answers to Merriam's (1900, p. 26) description; but the amount of red present is subject to some individual variation and is present in lesser amount in the younger individuals.

***Dicrostonyx rubricatus rubricatus* (Richardson)**

Alaska Collared Lemming (Ce-lum-me-tak)

Nos. 40119 to 40123 taken in February and March, 1928. These six specimens are topotypes of *Dicrostonyx hudsonius alascensis* Stone (1900, p. 37) which Allen (1919, p. 519) has placed as a synonym of *Dicrostonyx rubricatus rubricatus*. The animals are, of course, in the white winter coat and possess the curious enlargements on the nails of the forefeet.

***Microtus operarius endoeucus* Osgood**

Northern Tundra Vole

Nos. 40124 and 40125, taken in September, 1927, on river, fifty miles south of Barrow, Alaska. Mr. Brower remarks that he did not get the native Eskimo name of this species, and that the two specimens were the first he had ever seen. To the writer's knowledge, no specimen of this subspecies has before been recorded from so far north. For the subspecific determination of these two specimens, we are indebted to Dr. H. H. T. Jackson of the United States Bureau of Biological Survey.

## LITERATURE CITED

ALLEN, G. M.

1919. The American Collared Lemmings (*Dicrostonyx*). Bull. Mus. Comp. Zool., 62, 509-540, 1 pl.

BAILEY, A. M., and HENDEE, R. W.

1926. Notes on the mammals of northwestern Alaska. Jour. Mammalogy, 7, 9-28, pls. 2-4.

HOWELL, A. H.

1915. Revision of the American marmots. U. S. Dept. Agr., Bur. Biol. Surv., N. Am. Fauna, 37, 1-80, pls. 1-15, 3 figs. in text.

JACKSON, H. H. T.

1928. A taxonomic review of the American long-tailed shrews (Genera *Sorex* and *Microsorex*). U. S. Dept. Agr., Bur. Biol. Surv., N. Am. Fauna, 51, 1-238, pls. 1-12, 24 figs. in text.

MERRIAM, C. H.

1900. Papers from the Harriman Alaska expedition. I. Descriptions of twenty-six new mammals from Alaska and British North America. Proc. Wash. Acad. Sci., 2, 13-30.
1902. Four new Arctic foxes. Proc. Biol. Soc. Wash., 15, 167-172.

PREBLE, E. A.

1908. A biological investigation of the Athabaska-Mackenzie region. U. S. Dept. Agr., Bur. Biol. Surv., N. Am. Fauna, 27, 1-574, pls. 1-25, 16 figs. in text.

ROSS, B. H [= R].

1861. An account of the animals useful in an economic point of view to various Chipewyan tribes. Canad. Nat. and Geol., 6, 433-441.

STONE, W.

1900. Report on the birds and mammals obtained by the McIlhenny expedition to Pt. Barrow, Alaska. Proc. Acad. Nat. Sci. Phila., 1900, 4-49.

*Transmitted January 22, 1929.*



**PTERYLOGRAPHY OF CERTAIN NORTH  
AMERICAN WOODPECKERS**

**BY**

**WILLIAM HENRY BURT**

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY

Volume 30, No. 15, pp. 427-442, 7 figures in text

Issued June 18, 1929

UNIVERSITY OF CALIFORNIA PRESS

BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS

LONDON, ENGLAND

# PTERYLOGRAPHY OF CERTAIN NORTH AMERICAN WOODPECKERS

BY

WILLIAM HENRY BURT

(Contribution from the Museum of Vertebrate Zoology of the University of California)

---

## INTRODUCTION

In connection with a study of the morphology of the woodpeckers now under way, wet material representing most of the North American Recent genera of the Picidae has been accumulated, with the result that the writer has had opportunity to examine the pterylography of ten genera including twenty-three species and subspecies. This study revealed a marked uniformity of arrangement of feather pattern in the various genera. Many detailed differences are to be noted, but the general plan is the same in all the forms examined. Inasmuch as the pterylography of this group of birds seems never to have been studied adequately, it is thought desirable to publish a report at this time.

In his classic treatise on pterylography, Nitzsch (1840) figured *Picus viridis* and described briefly the following additional species: *Picus luridus* [= *Miglyptes tukki* (Less.)], *P. concretus* [= *Hemicercus concretus* (Temm.)], *P. tridactylus* [= *Picoides tridactylus* (Linn.)], *P. carolinus* [= *Centurus carolinus* (Linn.)], *P. martius* Linn., *P. bengalensis* [= *Brachypternus aurantius* (Linn.)], *P. auratus* [= *Colaptes auratus* (Linn.)], *P. macei* [= *Dendrocopos macii* (Vieill.)], and *P. medius* [= *Dryobates medius* (Linn.)]. Subsequent to this early date nothing was published until Shufeldt (1887), in a chapter on pterylography, described and figured *Dryobates villosus harrisi* and *Sphyrapicus varius nuchalis*. The figures were republished in 1888 with slight changes in the text. The specimens studied by the present writer do not agree, as indicated below, in all particulars with Shufeldt's figures, and it seems evident that, in his study of the plucked specimens, Shufeldt misinterpreted the exact positions of some of the feather tracts.

Another important work, dealing only with the wings, is that part of Steiner's (1918) careful study, relating to the Pici, in which he shows that the woodpeckers are eutaxic in the arrangement of the secondaries. There is considerable literature on the wings of birds, and Steiner gives a fairly complete list of the more important papers.

#### ACKNOWLEDGMENTS

To make this study possible it has been necessary to enlist the help of others in securing specimens from different localities. For their kind assistance in this particular the writer is greatly indebted to the following institutions and individuals: California Museum of Vertebrate Zoology, through several of its staff members; University of Kansas Museum, through Mr. Charles D. Bunker; Mr. Charles O. Handley; Mr. Donald D. McLean; Mr. James Moffitt; Mr. Charles E. Burt. The author also wishes to express his appreciation to Dr. Joseph Grinnell for helpful suggestions and criticisms concerning the study.

#### METHOD OF PROCEDURE

Nitzsch (1840, p. 24) employed three methods in examining feather tracts: (1) he plucked the bird and noted the pouches or pits in which the contour feathers were inserted; (2) he cut off the contour feathers close to their bases, and then wet the body; (3) he stripped off the skin and, after carefully cleaning it, examined it from the inside. Shufeldt (1887), in his studies, used the first method, that of plucking the bird and observing the pits or pouches where the contour feathers had been inserted. In the present study all three methods have been employed; that of cutting the feathers off was found most satisfactory. However, the exact outline of the tracts may be brought out much more clearly if, after cutting the feathers near the body, the bird is submerged in water. The feather stubs are buoyed up by the water and the positions of even the small down feathers become discernible. This method was employed with all of the species examined except *Picoides americanus americanus*. Since no specimens of this species were available in the flesh it was necessary to study a dried skin from the inside. Still another method used by many workers is to examine the young birds as the feathers are emerging. The last method has been used in the present study with *Colaptes auratus luteus*.

## CLASSIFICATION OF TRACTS

The classification of feather tracts here adopted is almost exclusively that of Boulton (1927). Boulton's classification, with some modification, was adopted from Nitzsch, Dwight, and Witherby. The apteria will be taken up but briefly in this paper.

The tracts and their subdivisions here recognized are as follows:

*Capital tract*: frontal region, coronal region, occipital region, superciliary region, loreal region, ocular region, malar region, auricular region, post-auricular region.

*Ventral tract*: inter-ramal region, submalar region, cervical region, sternal region, axillar region, outer abdominal region, inner abdominal region.

*Spinal tract*: cervical region, interscapular region, dorsal region, median pelvic region, lateral pelvic region.

*Lateral neck tract*.

*Caudal tract*: upper tail-coverts, rectrices, under tail-coverts, anal circlet, post-ventral region, oil gland tuft.

*Humeral tract*: outer humeral tract, inner humeral tract.

*Alar tract*: primaries, greater primary coverts, middle primary coverts, secondaries, greater secondary coverts, middle secondary coverts, carpal remex, carpal covert, lesser secondary coverts, marginal coverts, alula, alula coverts, carpometacarpal coverts, under greater primary coverts, under lesser primary coverts, under middle secondary coverts, under lesser secondary coverts.

*Femoral tract*.

*Crural tract*: external region, internal region.

## SPECIES EXAMINED

Because of the great uniformity in the general plan of feather arrangement in the family, it seems advisable to treat the group as a whole, pointing out such differences as do occur in the various forms. The following is a list of the species and subspecies examined:

1. *Colaptes auratus auratus* (Linnaeus). Yellow-shafted Flicker.
2. *Colaptes auratus luteus* Bangs. Northern Yellow-shafted Flicker.
3. *Colaptes cafer collaris* Vigors. Monterey Red-shafted Flicker.
4. *Ceophloeus pileatus pileatus* (Linnaeus). Eastern Pileated Woodpecker.
5. *Ceophloeus pileatus picinus* Bangs. Western Pileated Woodpecker.
6. *Centurus carolinus* (Linnaeus). Red-bellied Woodpecker.
7. *Centurus uropygialis uropygialis* Baird. Arizona Gila Woodpecker.
8. *Melanerpes erythrocephalus* (Linnaeus). Red-headed Woodpecker.
9. *Balanosphyra formicivora bairdi* (Ridgway). California Woodpecker.
10. *Asyndesmus lewisi* Riley. Lewis Woodpecker.
11. *Sphyrapicus varius varius* (Linnaeus). Yellow-bellied Sapsucker.
12. *Sphyrapicus varius nuchalis* Baird. Red-naped Sapsucker.
13. *Sphyrapicus ruber ruber* (Gmelin). Red-breasted Sapsucker.
14. *Sphyrapicus thyroideus thyroideus* (Cassin). Williamson Sapsucker.
15. *Dryobates villosus villosus* (Linnaeus). Eastern Hairy Woodpecker.



16. *Dryobates villosus orius* Oberholser. Sierra Hairy Woodpecker.
17. *Dryobates pubescens medianus* (Swainson). Eastern Downy Woodpecker.
18. *Dryobates pubescens turati* (Malherbe). Willow Downy Woodpecker.
19. *Dryobates scalaris cactophilus* Oberholser. Ladder-backed Woodpecker.
20. *Dryobates nuttallii* (Gambel). Nuttall Woodpecker.
21. *Dryobates borealis* (Vieillot). Red-cockaded Woodpecker.
22. *Xenopicus albolarvatus albolarvatus* (Cassin). White-headed Woodpecker.
23. *Picoides americanus americanus* Brehm. American Three-toed Woodpecker.

## DISCUSSION

*Capital tract.*—The frontal region is densely feathered. In every case the feathers extend down over the external nares, completely concealing them from view and thus protecting them from the entrance of foreign bodies. It is an interesting fact that the feathers cover the external nares more completely in the more arboreal forms such as the *Picoides* and *Dryobates* groups. Woodpeckers of these groups drill into bark and wood for a large proportion of their food, and bits of wood, bark, or other material, might easily fall into poorly protected nares. In forms where this protection is less needed, such as in the *Colaptes* and *Melanerpes* groups, the members of which depend to a large extent on food gathered from surfaces, the feathers do not cover the nares so completely. The frontal region is more sparsely feathered toward the mid-line, being divided in part by the median capital apterium in each genus except *Sphyrapicus*. The frontal region continues into the coronal region which, in turn, extends posteriorly over the head into the occipital region. The latter is divided in the mid-line by the median capital apterium. In *Sphyrapicus* the lower part of the coronal region is feathered across the middle and the feathers form a whorl-like pattern. The median capital apterium extends only part way down the occipital region, which is less densely feathered than the other parts of the capital tract.

The superciliary region consists of three or four indefinite rows of feathers which extend posteriorly from in front of the orbit back over the eye. The feathers of this region merge anteriorly and dorsally with the feathers of the coronal region, posteriorly with the feathers of the occipital region. The feathers of the loreal region are closely set and directed posteriorly. There is a series of small feathers on each lid of the ocular region.

The malar region extends anteriorly from directly beneath the ear opening, coming to a point on the lateral surface of the lower man-

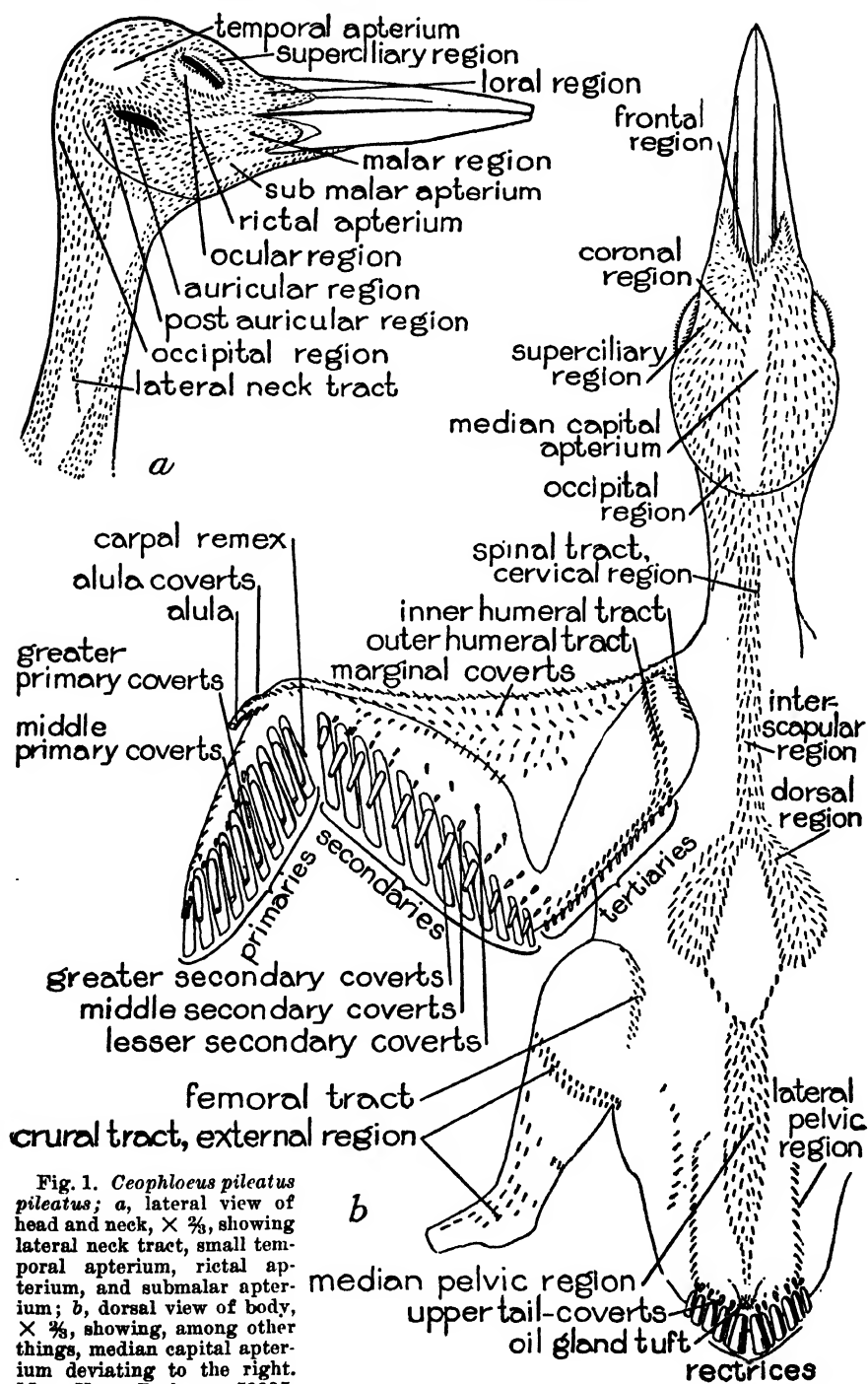


Fig. 1. *Ceophloeus pileatus*; a, lateral view of head and neck,  $\times \frac{2}{3}$ , showing lateral neck tract, small temporal apterium, rietal apterium, and submalar apterium; b, dorsal view of body,  $\times \frac{2}{3}$ , showing, among other things, median capital apterium deviating to the right. Mus. Vert. Zool. no. 53935.

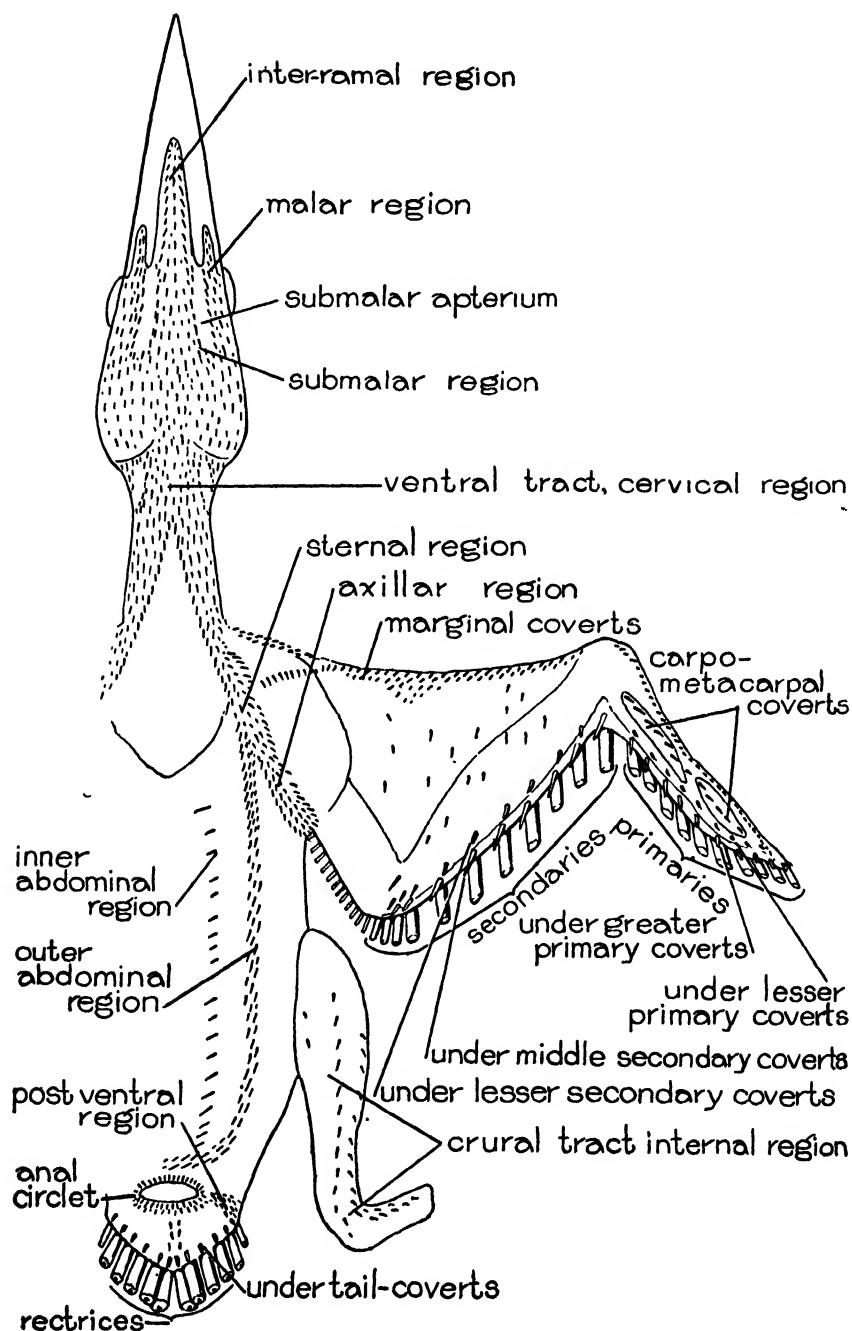


Fig. 2. *Ceophloeus pileatus pileatus*; ventral view of body,  $\times \frac{2}{3}$ , showing inner abdominal region and submalar apterium. Mus. Vert. Zool. no. 53935.

dible. The feathers of the median portion are directed posteriorly, those of the ventral and dorsal borders, ventrally and dorsally, respectively. Two rows of stiff feathers surround the ear opening in the auricular region; they are all directed postero-dorsally forming a funnel-shaped arrangement so as better to convey sound waves into the opening. The post-auricular region is continuous with the occipital region.

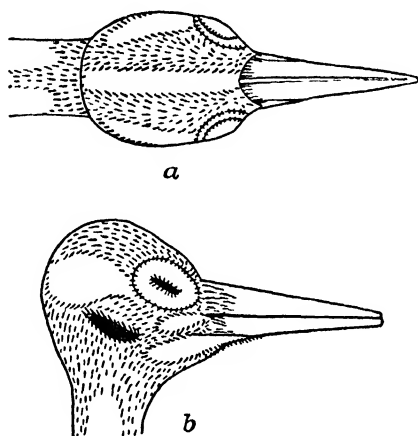


Fig. 3. *Dryobates nuttallii*; a, dorsal view of head,  $\times 1$ , showing relatively wide median capital apterium; b, lateral view of head,  $\times 1$ , showing relatively large temporal apterium and submalar apterium. Mus. Vert. Zool. no. 53932.

The apteria of the head are characteristic of the group. There are slight variations to be noted in the several genera as follows: The median capital apterium with its origin high up on the occiput, extends anteriorly over the top of the head and down the forehead nearly to the cranio-facial angle in all but *Sphyrapicus*. It varies somewhat in relative width and length in different genera (cf. figs. 1b, 3a, 4b). In *Colaptes*, *Ceophloeus*, and *Dryobates borealis*, the apterium deviates to the right of the mid-dorsal line as it passes down the forehead, thus following the course of the hyoid branches. In *Sphyrapicus* it is a short narrow apterium which extends anteriorly to the frontal region. Shufeldt (1888, p. 213) states that there is no median capital apterium in *Sphyrapicus*. He figures the form as having the head completely feathered. In every specimen thus far examined by the writer, there is a small median capital apterium and a prominent temporal apterium on each side of the head, as well as a distinct submalar apterium. It seems evident, therefore, that although a careful observer, Shufeldt, in his plucked specimens, failed

to see the finer details and the exact boundaries of the feather tracts. In *Sphyrapicus* the hyoid branches barely meet on the occiput and do not extend anteriorly over the head as in the other genera, but the apterium continues for a short distance beyond the termination of the hyoids. If, as appears to be the case, this apterium was brought about, in the evolution of the race, by the presence of the hyoid bones beneath the skin, through pressure or some other agency, it seems that the condition of shorter hyoids in *Sphyrapicus* is a reduction of what were at one time better developed structures, and that the vestige of an apterium is a character rapidly disappearing in *Sphyrapicus*. As far as known to the writer the median capital apterium is present only in birds with the hyoids greatly extended. Thompson (1901) figures the Giant Hummingbird (*Patagona gigas*) with a median capital apterium, and a specimen of the Black-chinned Hummingbird (*Archilochus alexandri*) at hand has a distinct median capital apterium. Hummingbirds, like woodpeckers, have the hyoids greatly extended.

Temporal apteria are present in every specimen examined. They are proportionately smallest in *Ceophloeus*, largest in *Dryobates* (cf. figs. 1a and 3b). They are intermediate in size in the other genera.

In addition to the above-mentioned apteria of the head region, there is a well defined apterium along the ventral edge of each mandible between the maxillary region and the inter-ramal region. It extends posteriorly to a point beneath the anterior border of the ear opening. This apterium is relatively smaller in *Ceophloeus*, whereas in *Dryobates* it is proportionately more extensive than in the other genera. I propose for it the designation Malar Apterium. A narrow apterium also extends back from the angle of the mouth (fig. 1a), and this may be known as the Rictal Apterium.

*Ventral tract.*—The inter-ramal, submalar, and ventral cervical regions are not separable except by their relative positions. The first occupies an anterior position, the second and third are successively posterior. The median portion of the inter-ramal region is feathered. There are narrow marginal spaces in *Ceophloeus*, which are slightly wider in the other genera. The submalar region is continuous, at its posterior boundary, with the post-auricular region.

About midway down the neck the ventral cervical tract bifurcates and a branch passes to either side. In the sternal region each of these branches in turn gives rise to a smaller branch which unites dorsally

with the alar tract. The main branches, however, pass posteriorly as broad ventral bands on either side of the body. At a point near the level of the fork of the furcula, each sternal branch divides again into a broad axillar and a narrow outer abdominal region. The axillar region, made up of six or seven rows of feathers, extends postero-laterally and dorsally, terminating in a pointed "hook" behind the wing. In *Sphyrapicus* a single row of feathers, continuous with the "hook" near its point, passes anteriorly for a short distance lateral to the large pectoral muscle. The anterior portion of the outer abdominal region of the ventral tract consists of one indistinct and two distinct rows of feathers which expand into four or five rows anterior to the anal region. The two branches converge posteriorly and meet anterior to the anal circlelet.

There is, in addition to the above-mentioned ventral regions, a single definite row of feathers on each side of the mid-ventral line (figs. 2 and 4a). They are more mesial than the outer abdominal regions just discussed. Anteriorly, these arise at the furcula, pass posteriorly parallel with the tracts of the outer abdominal regions and merge with the latter at their posterior limits. The single rows of feathers are here designated as Inner Abdominal Regions. The feathers are of a downy character and all are directed mesially, covering in part the median abdominal apterium. This region was not mentioned by Nitzsch (1840) in his work, nor by Shufeldt (1888) in his description of the pterylography of the woodpeckers.

*Spinal tract.*—The cervical region of the spinal tract is a continuation of the occipital region. At a point about midway down the neck two small branches are given off, one to either side of the neck (fig. 1a). These lateral neck tracts pass postero-ventrally, almost reaching the sternal branches of the ventral tract. The spinal tract continues posteriorly through the interscapular region as a narrow strip made up of four or five rows of feathers. Between the level of the tips of the scapulae, the dorsal region bifurcates, and each branch expands postero-laterally into a lobate tract (figs. 1b and 4b). This bilobate condition is uniform in all the specimens examined. However, Shufeldt (1888, p. 217) figured *Sphyrapicus varius nuchalis* as having the spinal tract continuous, with an expansion or "lozenge-shaped area" in the dorsal region. Specimens at hand, of *Sphyrapicus*, all reveal the normal bilobate condition of the dorsal region, and therein do not agree with the figures of Shufeldt (*loc. cit.*).

The posterior tip of each lobe of the dorsal region connects with the median pelvic region by a single row of feathers. The median pelvic region begins anteriorly as a narrow pointed tract, expands over the rump, and terminates posteriorly in a point dorsal to the

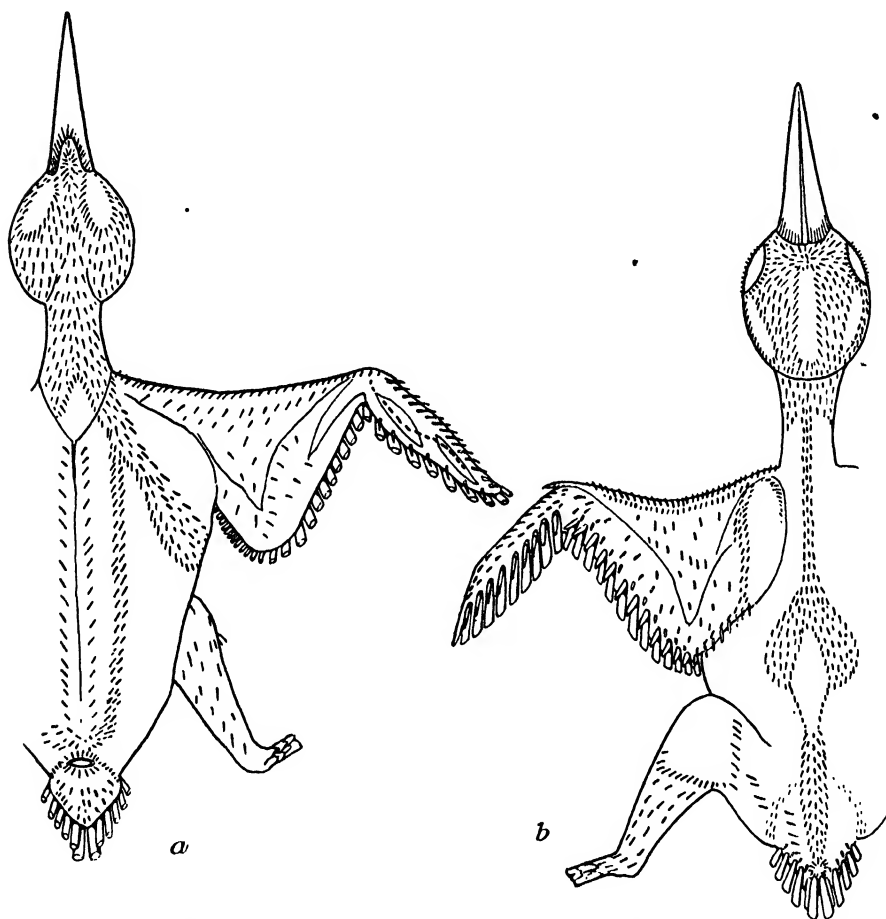


Fig. 4. *Sphyrapicus ruber ruber*; a, ventral view of body,  $\times \frac{3}{4}$ , showing submalar apertures and inner abdominal region; b, dorsal view of body,  $\times \frac{3}{4}$ , showing reduced median capital apertures, prominent temporal apertures, and bilobate dorsal region of spinal tract (cf. Shufeldt, 1888, p. 217, fig. 5). Mus. Vert. Zool. no. 53934.

oil gland. To either side of the median pelvic region there is a small tract of feathers that arises posterior to the lateral upper tail coverts and passes anteriorly for about half the length of the pelvic region. This tract is made up of one or two rows of feathers and is here designated as the Lateral Pelvic Region.

**Caudal tract.**—There are twelve rectrices in most woodpeckers. The middle, or first, pair usually is somewhat greater in diameter of shaft than the more lateral feathers. This is especially true in such genera as *Sphyrapicus*, *Dryobates*, *Xenopicus*, and *Picoides*. These forms spend a large proportion of their time on trunks of trees while in search of food and thereby make greater use of the tail feathers as a prop. On the other hand, in such forms as *Colaptes*,

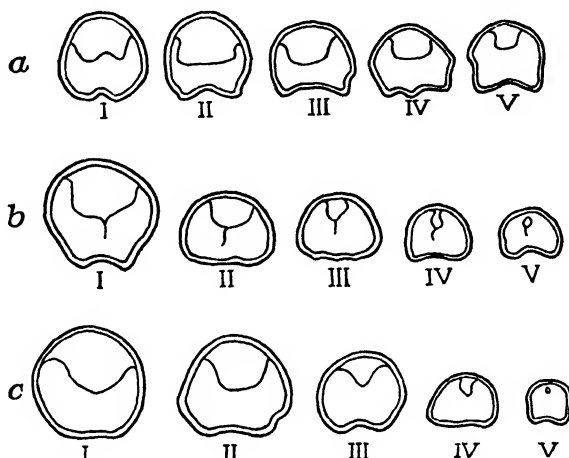


Fig. 5. Cross-sections of the first five right rectrices of three genera of Woodpeckers. *a*, *Colaptes*; *b*, *Balanosphyra*; *c*, *Dryobates*. The median rectrices of the three genera are corrected to a standard length of 72 mm. The relative diameters of the rectrices here shown are corrected in the same ratio. Note progressive increase in size of rectrices I and II with a reduction in size of rectrices IV and V as shown from top to bottom of the series.

where much time in search of food is spent on the ground and the tail is not so extensively used as a prop, the middle feathers are only slightly, if any, larger than the pair adjoining them. Thus the series grades down gradually, in diameter of shaft, from the first to the fifth pair (fig. 5). The outermost, or sixth tail feather, is usually much reduced in all forms and occurs only as a vestige which lies somewhat dorsal to the fifth pair and assumes the position of a covert rather than that of a tail feather. In speaking of the outermost, or sixth, pair of rectrices in the woodpeckers and wrynecks, Miller (1915, p. 137) says: "It is of interest to find that this pair of small rectrices, heretofore supposed to be invariably present, has been lost by *Campephilus pollens* and its place taken by the much reduced fifth pair."

There are twelve upper tail-coverts. The reduced median pair migrates laterally and each covert eventually lies lateral instead of



dorsal to its respective tail feather. This migratory aspect is demonstrated in the early stages of the development of the feathers in *Colaptes* (fig. 6). In the embryo the papillae of the upper tail-coverts may be seen lying directly dorsal to the papillae of the respective rectrices. In the adult the median upper tail-coverts no longer lie dorsal to their respective rectrices but lateral to them. There are twelve under tail-coverts. The median pair is reduced to downy vestiges. To either side, a row of feathers extends forward from the lateral under tail-coverts, passes along the ventro-lateral portion of the pygostyle and joins the anal circlet. This is designated as the

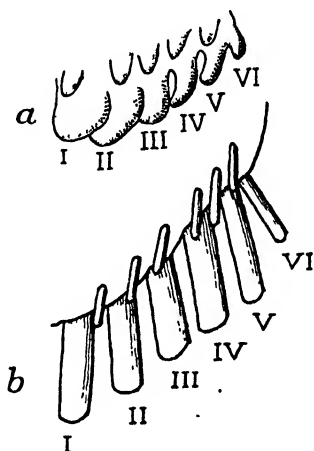


Fig. 6. Right rectrices and upper tail-coverts of *Colaptes auratus luteus*, showing displacement of median upper tail-coverts. *a*, A 17-mm. embryo showing median upper tail covert lying dorsal to tail feather no. I, Mus. Vert. Zool. no. 53943; *b*, adult,  $\times 4$ , showing the lateral migration of the median upper tail-coverts, Mus. Vert. Zool. no. 53942.

post-ventral tract by Shufeldt (1887), and here designated as the Post-ventral Region. There is also a small tuft of feathers on the mid-ventral portion of the pygostyle. The oil gland is tufted. The caudal tract is uniform throughout the group with respect to distribution of feathers, but in the relative diameters of the central rectrices there is considerable variation (fig. 5).

**Humeral tract.**—The outer humeral tract arises in the shoulder region from the marginal coverts, crosses dorsal to the humerus, takes a spiral course, and continues down the posterior border of the humerus nearly to the distal end as a double row of feathers which includes the tertiaries.

**Inner humeral tract.**—An inner humeral tract arising with, but proximal to, the humeral tract, passes back across the proximal end

of the humerus for a short distance. This tract is least evident in *Dryobates nuttallii*, where it is but a single row of feathers. Nitzsch (1840) reports this tract absent in *Picus luridus*, this being the only woodpecker in which it is reported absent as far as known to the writer.

*Alar tract*.—There are eleven primaries; the most distal, or eleventh, is much reduced but present in all forms examined. Miller (1915, p. 135) in this connection gives the following:

My determination of the number of primaries differs from the figures given by Gadow (Tierreich, 1893) in the case of the Pigeons, Bee-eaters, Rollers, Barbets, Toucans, and Woodpeckers. . . . In the typical Rollers and the three families of Pici above mentioned there is in each case a minute vestigial eleventh primary.

The present findings bear out Miller's observations. Ten greater primary coverts are present and each lies distal to its respective primary. A covert for the eleventh primary is not present. The number of middle primary coverts varies from six to nine. It is always the first, or most proximal, of the middle coverts that are missing when the number is reduced. The variation in number occurs not only between different species, but among individuals of the same species. The middle primary coverts alternate with the greater primary coverts and lie directly above their respective primaries.

Concerning the alula quills, Miller (1915, p. 136) states that: "many woodpeckers (as *Centurus* and *Dryobates*) and small Oscines have but three, of which the third is small." There are four alula quills in each of the forms examined by the writer, except *Dryobates nuttallii*, where there are but three.

There are eleven secondaries present in each specimen examined. The eleventh, or most proximal, secondary is often much reduced. The greater secondary coverts cross the secondaries obliquely with the point of insertion proximal to the secondary. The much reduced carpal remex is present in all the forms studied. There is no carpal covert. The lesser secondary coverts lie parallel to the secondaries. The remaining feathers, the under primary coverts, and the under secondary coverts are arranged over their respective primaries and secondaries.

*Femoral tract*.—This is a weak tract consisting of a single row of feathers which extends across the mid-portion of the femur at nearly right angles to the shaft of the bone.

*Crural tract*.—The external region consists of a band of strong feathers extending from the region of the cnemial crest across the

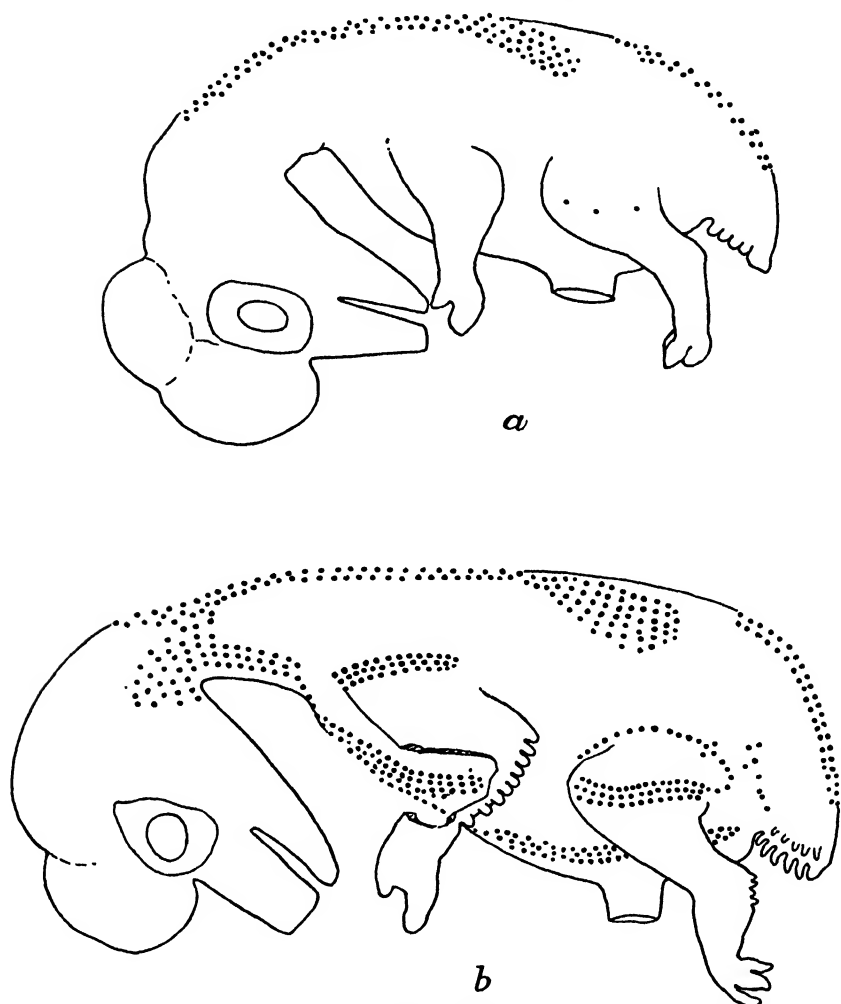


Fig. 7.—Embryos of *Colaptes auratus luteus* showing relative time of emergence of certain feather tracts. *a*, A 13.5-mm. embryo showing spinal tract, three papillae on crural tract, and first five rectrices, Mus. Vert. Zool. no. 43955; *b*, a 17-mm. embryo showing, in addition to the first stage, the outermost tail feathers, first five upper tail-coverts, ventral tract extending anteriorly through the cervical region, humeral tract, secondaries, crural tract, femoral tract, and posterior margin of capital tract, Mus. Vert. Zool. no. 53943.

outer surface of the leg, roughly forming a semicircle. A few smaller feathers are distributed irregularly over the distal portion of the tibio-tarsus. The internal region is sparsely and irregularly feathered with small feathers. Anteriorly the feathers extend down onto the tarsus for a short distance.

Embryos of *Colaptes auratus luteus* taken from the egg show the succession of certain feather tracts. Only two stages are represented

in the specimens at hand (fig. 7). The first stage, a 13.5-mm. embryo, shows only the spinal tract, three papillae on the crural tract, and the first five pairs of rectrices. The next stage, a 17-mm. embryo, shows, in addition to the first stage, the outermost or sixth tail feather, the first five pairs of upper tail-coverts, the under tail-coverts, the ventral tract anterior to and including the cervical region, the humeral tract, secondaries, well outlined crural and femoral tracts, and the posterior margin of the capital tract. As shown by these two stages, the median body tracts appear first. Likewise, in the wing the sequence is from proximal to distal portions. The head region is among the last to be feathered. If this be of phylogenetic significance it would indicate the appearance of feathers first near the central axis of the trunk, then progressively outward to more distal portions.

### SUMMARY AND CONCLUSIONS

The North American woodpeckers, as a group, are remarkably uniform in the general distribution of feathers over the body. Each possesses a median capital apterium, though it is much reduced in *Sphyrapicus*. A temporal apterium is always present on the side of the head. There is a paired submalar apterium. A lateral neck tract branches off from the spinal tract. A dorsal tract branches into two lobate areas which are connected with the pelvic region by a single row of feathers. An inner humeral tract is present, except for *Picus luridus* (cf. Nitzsch, 1840). The wings are eutaxic. An eleventh primary, much reduced, is present. In the rectrices, twelve in number, the outermost pair is always reduced to a functionless vestige and may even be altogether wanting. The median pair is variously modified in different forms. This pair is best developed in those woodpeckers which use the tail most extensively as a prop and which search the tree trunks for food, and less developed in forms in which the tail is used relatively little as a prop. An enlargement of the central rectrices is always correlated with a reduction of the lateral ones. There is a single row of feathers on each side of the mid-ventral line, here described for the first time in the woodpeckers, and termed the Inner Abdominal Region.

In so far as the studies recounted in this paper show, the feather arrangement in the woodpeckers is of significant taxonomic value mainly in distinguishing the order. However, *Sphyrapicus*, an

aberrant genus, is readily distinguishable from the other genera by the feather arrangement. Specific differences are of slight amount and are somewhat variable. Adaptive modifications are to be found in the individual feathers as well as in the endoskeleton, muscles, and other soft parts. This is shown by the differing degrees of development in the central rectrices with corresponding reduction of the lateral ones, a specialization which is closely correlated with the special habits of these birds.

### LITERATURE CITED

- BOULTON, R.  
1927. Ptilosis of the house wren (*Troglodytes aedon aedon*). *Auk*, 44, 387-414, 12 figs. in text.
- MILLER, W. DEW.  
1915. Notes on ptilosis, with special reference to the feathering of the wing. *Bull. Am. Mus. Nat. Hist.*, 34, 129-140.
- NITZSCH, C. L.  
1840. *System der Pterylographie*. Halle, Eduard Anton, 1-228, 10 pls.
- SCLATER, P. L.  
1890. Remarks on the fifth cubital remex of the wing in Carinatae. *Ibis*, 2, 77-83.
- SHUFFELDT, R. W.  
1887. A chapter on pterylography. *Forest and Stream*, Aug. 25, 1887, 84-85, 4 figs. in text.  
1888. Observations on the pterylosis of certain Picidae. *Auk*, 5, no. 2, 212-218, 4 figs. in text.
- STEINER, H.  
1918. Das Problem der Diastataxie des Vogelflügels. *Jenaische Zeitschrift für Naturwissenschaft*, 55, 221-496, 3 pls., 49 figs. in text.
- THOMPSON, D'ARCY W.  
1901. On the pterylosis of the giant humming-bird (*Patagona gigas*). *Proc. Zool. Soc. London*, 1901, 311-324, 6 figs. in text.

*Transmitted March 2, 1929.*





NOTES ON THE GENUS ENSATINA IN  
CALIFORNIA, WITH DESCRIPTION OF A  
NEW SPECIES FROM THE SIERRA NEVADA

BY

TRACY I. STORER



UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 16, pp. 443-452  
Issued June 18, 1929

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

NOTES ON  
THE GENUS *ENSATINA* IN CALIFORNIA, WITH  
DESCRIPTION OF A NEW SPECIES  
FROM THE SIERRA NEVADA

BY

TRACY I. STORER

(Contribution from the Division of Zoology, College of Agriculture, University of California)

The genus *Ensatina* Gray, 1850, save for one little-known species, *E. platensis* (Espada) of southern South America, is confined to the extreme western portion of North America, west of the Cascade-Sierra Nevada divide, from the vicinity of Puget Sound to extreme southern California. Two species have currently been recognized here, *Ensatina croceator* (Cope) in the Sierra Nevada and *E. eschscholtzii* Gray in the Coast Ranges and northerly. Recent opportunity to examine additional material, especially in the assemblage heretofore designated as "*croceator*," has prompted a review of the standing of the genus in California.

Since this examination was completed there has appeared a paper by Dunn (1929) designating the heavily blotched form of the southern mountains as *Ensatina klauberi*. While it is obvious that at least three members of the genus must be recognized in California, my studies indicate that the coastal and southern forms are already provided with names, leaving the Sierran form as the one to be named, and this I will do below.

***Ensatina croceator* (Cope)**

*Type*.—No. 4701, U. S. National Museum [now lost]; collected by John Xantus.

*Type locality*.—Fort Tejon [Kern County], California.

*Diagnosis*.—Size moderate among California salamanders, total length up to 150 millimeters (nearly 6 inches); naso-labial grooves developed; costal folds 10 (rarely 11); maxillary and mandibular teeth small; vomerine teeth on two quadrants meeting medially; parasphenoid teeth in two elongate separate patches, slightly divergent posteriorly; body coloration sharply bi-color, black with large patches of orange-rufous; a broad band (slightly angular anteriorly) across occiput, often joining spots on eyelids; limbs orange yellow, save at tips where dusky.

Cope in 1867 (pp. 210–211) described a heavily blotched species of salamander, *Plethodon croceater*, on the basis of one specimen, no. 4701, U. S. National Museum, stated to have been collected by John Xantus at Fort Tejon, California. Lockington (1880, p. 295) reported one individual collected “about seventy-five miles south-east of San Diego,” in California. The type disappeared prior to 1880 and the whereabouts of Lockington’s specimen if extant is at present not known. Cope in 1889 (p. 151) mentioned a specimen from Cape St. Lucas, Lower California, and another from near San Diego. Van Denburgh (1916, pp. 220–222) has expressed doubt concerning the Cape record and has suggested that Cope’s second record referred to Lockington’s specimen.

There are two specimens of *croceater* which for many years have been in the collection of the University of California, first in the Department of Zoology and more recently in the Museum of Vertebrate Zoology (nos. 8243, 8244). Grinnell and Camp (1917, p. 132) considered one of these the probable type of the species. The original description mentioned specifically an individual specimen. No specimen of this number or, indeed, any example of *croceater* could be found in the National Museum collection by Camp in 1915 nor by myself in 1927. The loose tag which accompanied the two specimens at Berkeley (which I first saw in 1911) bears the legend “*Plethodon croceater* Cope | Ft. Tejon Cala.” No date or collector is indicated. Specimens of birds collected by Xantus in Lower California in 1860 and now in the collection of the Museum of Vertebrate Zoology carry “Smithsonian” labels, with locality and year of capture. So far as I can ascertain there are no other early specimens of amphibians from Fort Tejon in the University collections. Had these specimens been the types the fact would probably have been indicated in some way on the bottle label (as was done for the type of *Xantusia riversiana*, which was in that collection) and some reference to the location of the type would probably have appeared in Cope’s “Batrachia.” I have searched the early records of gifts to the University without being able to get any clue to the source of these specimens. The original description was published in 1867, the University at Berkeley was established in 1869, so that collections were not begun until the latter year, a fact which adds further doubt to the status of these as types. Furthermore, the lack of an original label and the nature of the associated tag (of drawing paper, such as has been used more recently in the University) raises a doubt in my mind

as to whether these examples ever actually came from Fort Tejon or whether they may not have been obtained from some now unknown locality in the southern mountains and have been given the label after identification through the use of Cope's "Batrachia." Finally, neither of these specimens (although both are and have been badly shrunken ever since I first saw them) seems ever to have been large enough to have agreed with Cope's measurements of his type, which was nearly 6 inches in length. Their claims to typeship must therefore be discarded, and the type specimen considered to be lost.

This leaves the question of identification and of type locality dependent entirely upon the original description. This, fortunately, is adequate and I see no reason to doubt the type locality, although the type specimen may actually have been secured at some slightly higher station in the general neighborhood of Fort Tejon.

Since Lockington's time and until just recently, no specimens of *Ensatina croceator* have been reported from the southern Sierras of California, the name meanwhile having been applied to spotted "Plethodons" from the Sierra Nevada. Klauber in 1927 (pp. 2-4) published a brief paper listing five specimens of *croceator* from San Diego County, two from the Cuyamaca Mountains, one from one mile northwest of Big Laguna in the Laguna Mountains, and two from Descanso. He also listed two from the San Jacinto Mountains, collected by Frank Stephens on April 21, 1903, but not previously reported upon. On October 1, 1927, a specimen was taken at Crystal Creek, San Bernardino Mountains, by Edmund C. Jaeger and sent to me for identification. Recently Willis G. Craig, collecting with S. S. Berry on Hot Springs Mountain near Warner's Hot Springs, San Diego County, secured eight specimens, two of which I received for identification. These were taken on April 5, 1928, at an altitude of about 4500 feet. L. Walker obtained a specimen (48 mm. long) at Idylwild, San Jacinto Mountains, on April 29, 1928, and specimens were taken in San Diego County at Descanso on April 1, 1928, by Joe Carter and at Pine Valley by F. W. Kelsey on the same date. Several have been taken at Julian (see table of measurements). Dunn (1929) lists two from "Mill Canyon, near Banning," 5500 feet. This would place the record very close to San Bernardino Mountain proper, in San Bernardino (not Riverside) County, and in the San Bernardino (rather than San Jacinto) Mountains. Dunn also lists one from Rose Mine, Laguna Mountains. L. M. Klauber (MS) reports having taken a specimen of *croceator* from the Laguna Hanson Mountains, 55 miles southeast of San Diego.

TABLE 1  
MEASUREMENTS, IN MILLIMETERS, OF SPECIMENS OF *Ensatina croceata* FROM SOUTHERN CALIFORNIA

| Coll and No     | Sex | Locality  | Date           | Total length | Length of tail | Snout to gular fold | Greatest width of head | Orbit | Inter-orbital space | Fore-leg | Hand | Axilla to groin | Hind leg | Hind foot |
|-----------------|-----|---|----------------|--------------|----------------|---------------------|------------------------|-------|---------------------|----------|------|-----------------|----------|-----------|
| U.S.N.M. 4701   |     | Fort Tejon, Cala., John Xantus  | 1860           | 150          |                | 16 7                | 14 2                   | 4 6   |                     |          |      |                 |          |           |
| L.M.K. 1174     | ♀   | Julian, San Diego Co., Calif.   | July 25, 1927  | 132          | 55             | 19 5                | 13                     | 5 0   | 4 0                 | 22 0     | 8 0  | 40 0            | 25 3     | 11 4      |
| L.M.K. 1176     | ♀   | Julian, San Diego Co., Calif.   | July 25, 1927  | 131          | 56             | 18 5                | 12                     | 5 3   | 4 0                 | 20 5     | 8 0  | 37 0            | 24       | 11 0      |
| S.D.S.N.H. 1149 |     | San Jacinto Mts., Calif., F. Stephens                                 | April 21, 1903 | 130±         | 62±            | 17 6                | 12                     | 4 6   | 4 2                 | 21 5     | 8 4  | 28 0            | 21 8     | 12 0      |
| U.S.N.M. 75229  | ♂   | Mill Creek, 5500 feet, San Bernardino Mountains, Pierce and Gilman    |                | 130          | 65             | 15                  |                        |       |                     |          |      |                 |          |           |
| L.M.K. 589      | ♀   | Descanso, San Diego Co., Calif., Joe Carter                           | April 1, 1928  | 128          | 54             | 19                  | 13 2                   | 4 5   | 4 0                 | 22 2     | 8 2  | 37 0            | 24 0     | 11 0      |
| U.S.N.M. 75337  | ♀   | Descanso, San Diego Co., Calif., Joe Carter                           | April 1, 1928  | 127          | 54             | 19 5                |                        |       |                     |          |      |                 |          |           |
| T.I.S. . . .    |     | Crystal Creek, north side, San Bernardino Mountains, Edmund C. Jaeger | Oct. 1, 1927   | 111          | 53             | 17 5                | 10 4                   | 4 5   | 3                   | 18 2     | 7 7  | 26 3            | 21 0     | 9 5       |
| L.M.K. 1175     |     | Julian, San Diego Co., Calif.   | July 25, 1927  | 110          | 45             | 18                  | 11                     | 5 0   | 3 4                 | 21 3     | 7 6  | 31 9            | 21 6     | 10 7      |

Summarizing the available data, *Ensatina croceater* proves, on the basis of current specimens, to range from the north slope of the San Bernardino Mountains through the San Jacinto Mountains at least to Pine Valley, San Diego County. The type locality is in the Upper Sonoran Zone as are some of the recent localities of record, others being in the Transition Zone. With Van Denburgh (1916) I hold the Cape San Lucas record "exceedingly dubious."

The type locality lies northwesterly nearly one hundred miles from the most northerly of the records cited above. This would indicate the desirability of searching for representatives of this species in the mountains connecting the San Bernardino and Tehachapi ranges.

The recent activity of L. M. Klauber and his associates interested in herpetology in the southern counties is responsible for the number of individuals of this species which have come to hand in the past two years. It is a matter of regret, therefore, that I find it necessary to reduce the name proposed by Dunn for the southern form to synonymy under *croceater*. Comparison of the original descriptions of *croceater* and *klauberi* with specimens as listed above leaves no doubt that we are dealing with a single species. The striking color pattern, stout bodily form, and large size, all of which were indicated by Cope (1867), make it impossible to question the applicability of his name to the above material. A single feature of difference between the descriptions of Cope and Dunn and the material which I have seen is in the number of costal grooves and folds. I find 10 folds (11 grooves) on all save two; one of these has apparently 11 folds (12 grooves) on each side and two have 10-11 (11-12).

One of the specimens collected by Mr. Klauber near Julian on July 25, 1927, was accompanied by a group of fourteen eggs. These adhered to one another, but exhibited no evidence of a stalk. Individually they were about five-sixteenths of an inch in diameter, yellowish in color, and opaque. The form and the time of deposition as indicated by this isolated instance agree with our knowledge of the breeding habits of *eschscholtzii* in northern California.

Specimens of a spotted salamander from various localities in the Sierra Nevada of California have during the past decade been held to represent *Ensatina croceater* (see Van Denburgh, 1916; Grinnell and Camp, 1917; Storer, 1925; Dunn, 1926). Recent capture of numerous specimens of an *Ensatina* in the mountains of southern

California shows, upon study of the original description of *Plethodon* [= *Ensatina*] *croceator* Cope, that all the animals from Fort Tejon southward belong to that species and that the form from the Sierra Nevada, being neither *croceator* nor *eschschooltzii*, therefore requires naming. It may be called

***Ensatina sierrae*, new species**

Sierra Nevada Salamander

*Type*.—No. 10202, Museum of Vertebrate Zoology, University of California; collected by L. K. Wilson, July 11, 1925.

*Type locality*.—Yosemite Valley, Mariposa County, California; actually at 7300 feet, near Dewey Point, on south rim of valley.

*Diagnosis*.—General form like that of other members of the genus *Ensatina*; intermediate in size between *eschschooltzii* and *croceator*; very close to *platensis* in external appearance; dorsal coloration blackish or dark seal brown, marked with numerous large and small rounded spots (seldom over 4 mm. in diameter) of reddish brown; adjacent spots not often confluent; undersurface dusky yellow.

The description of "*croceator*" in my 1925 synopsis and in Dunn's 1926 volume being based upon what is here characterized as *sierrae*, I deem it unnecessary to offer further description of the new species.

Four living specimens of *sierrae* from Sly Park, Eldorado County, altitude 3500 feet, collected about May 6, 1928, indicate that in *sierrae* there are changes in coloration with change in size, less of the bright color being present on the younger individuals. The color comparisons below are based upon Ridgway (1912).

The smallest individual (approximately 40 millimeters in total length) shows light orange buff on the dorsal and posterior surfaces of upper "arm" and thigh. The body is otherwise practically black, with a heavy sprinkling of fine leucophores over the entire dorsal and lateral surfaces, including extremities. Upon close scrutiny under the binocular microscope a few very small areas of the reddish coloration of the adult animal are to be seen, on the tail and eyelids particularly.

The next size stage (55–60 mm.) shows an increase of the red element in the coloration, the arm and thigh areas are brighter and more extensive, near raw sienna in color, and the dorsal surface is blackish brown, but the fine white markings are still present. The eyelids are colored like the thighs though slightly duller, and there is a narrow patch of this color dorsally where the tail joins the body.

The next two individuals are 95 and 107 millimeters respectively in length. The body dorsally is light seal brown, the arms and thighs close to flame scarlet as are the scattered irregular spots up to 4 mm. in length on the tail. There are scattered fine markings of this color on the sides of body and head and the eyelids are ferruginous. The ventral surface is less dusky than in the smaller animals and a smaller proportion of minute leucophores is to be seen on the dorsum. The 94-mm. specimen is even more brightly marked than the larger one.

The range of *Ensatina sierrae* lies chiefly if not exclusively within the Transition Zone of the Sierra Nevada, and extends at least from Tulare County to Eldorado County, and may extend farther north (see Slevin, 1928). Specimens have been examined from the following localities: Sly Park, Eldorado County, 3500 feet altitude, 4; Yosemite Valley, Mariposa County, 4000 feet, and the type locality, 7300 feet, 5; North Fork, Madera County, 3000 feet, 4; Giant Forest, Tulare County, 6000 feet, 2; 4 miles southwest of Nelson, Tulare County, 1.

A feature arguing for specific distinctness between *sierrae* and *croceator* is that the young of the former are marked with fine white dots and acquire the reddish blotches with increasing size, whereas the small young of *croceator* (one at hand of 38 millimeters total length) exhibit the characteristic sharp-edged transverse light patches in almost equal proportion to those seen on the adult.

*Sierrae*, as indicated by specimens at hand, occupies a somewhat higher zonal position than *croceator*, although additional specimens may serve to lessen the discrepancy here indicated. A part if not all of the population of *sierrae* resides in an area where freezing temperatures are experienced over a considerable period during the winter months, while the habitat of *croceator* is somewhat warmer.

### *Ensatina eschscholtzii* Gray

*Type*.—None designated; in British Museum (see Boulenger, 1882, p. 55).

*Type locality*.—California [=Monterey: see Boulenger, 1882, p. 55].

*Diagnosis*.—Dorsal coloration of body solidly dark reddish brown or finely mottled, but without rounded spots or squarish blotches; young sometimes with minute pinpoints of lighter color on dorsal surface; form usually less robust than in *sierrae* and much less so than in *croceator*.

For several years it has been evident to me that the individuals of "*eschscholtzii*" from Berkeley and vicinity were different from those of the north coast country. The north humid coast belt individuals are in general more delicate of structure and slenderer, and their coloration tends to be mottled especially where the darker dorsal coloration joins the paler color of the undersurface. The intercostal furrows are often invaded by lighter color and the proximal segments of the limbs are patterned with the darker dorsal color. The Berkeley individuals are often nearly bi-color with a rather sharp distinction between the darker dorsal and paler ventral color. In life these colors are respectively dark reddish brown and dull yellow; in preservative the upper surface becomes dark bluish gray. Were these distinctions not crossed elsewhere there would be warrant for separating the northern population under the revived name *oregonensis* Girard, 1856, while continuing to designate the specimens from central coastal California as *eschscholtzii*. There are, however, two examples of *eschscholtzii* from Sierra Madre, Los Angeles County,



and Forest Home in the San Bernardino Mountains, which have a mottled scheme of coloration, and I deem it better, therefore, until more, well preserved, material is at hand, to continue use of the name *eschschooltzii* for the whole aggregation.

New localities of record for *Ensatina eschschooltzii* include importantly an extension of range to San Diego County. A specimen, previously reported as *Aneides lugubris* (Stephens, 1921, p. 59), which I examined on May 8, 1929, proves to be an *Ensatina* and of the species *eschschooltzii* and not *croceater* as might be expected. The full data are "Sequoia Mine, 33 mi. e. or n.e. of San Diego, Cal. J. T. Worthington 1 July 1920, no. 259, F. Stephens." The specimen is no. 6 in the collection of the Museum of the San Diego Society of Natural History. At my request Mr. L. M. Klauber undertook to locate the mine in question but present county records afforded no clew. In appearance the specimen resembles individuals from the San Francisco Bay region. One specimen in the collection of the American Museum of Natural History (no. 55879) from San Benito County indicates that the range of this species southward in the Coast Ranges will be found to be practically continuous when adequate collecting is done in the south central coast region. Another in the same collection (A.M.N.H. no. 5351) is from Verdugo Cañon near Glendale, Los Angeles County. *Eschschooltzii*, therefore, as here broadly defined, ranges from northern Washington to southern California.

Dunn's statement (1926, p. 189) of range is too extensive. The Lockington record (listed by him under *eschschooltzii*, p. 195) pertains to *croceater*, and "Fresno" (which is in the San Joaquin and not the Sacramento Valley) as a locality of record based upon material collected by Eisen (U.S.N.M. no. 11764, 17650-2) is a puzzle. So far as known to me no plethodontids occur or have occurred on the flat "plains" area of the Sacramento-San Joaquin basin (save for two records of *Batrachoseps attenuatus* where possibly carried down by winter floods). Some at least of Eisen's "Fresno" material was undoubtedly collected in the adjacent hills, miles distant and in a different zonal and faunal area. Furthermore, this ascribes *eschschooltzii* to a region heretofore considered to harbor only a spotted species (*sierrae*).

### SUMMARY

Three species of *Ensatina* are found to inhabit the Pacific Coast of North America, *croceater*, a large blotched species ranging in California from the Tehachapi region south to the Mexican boundary and possibly beyond, *sierrae*, a spotted form in the Sierra Nevada, and *eschschooltzii*, in the coastal region from Washington to extreme southern California. This last may be a composite, later to be resolved into a southern form, *eschschooltzii*, and a northern form, *oregonensis*, the latter possibly integrating with *sierrae*.

## LITERATURE CITED

BOULENGER, G. A.

1882. Catalogue of the Batrachia Gradientia s. Caudata and Batrachia Apoda in the collection of the British Museum (ed. 2; London, printed by order of the trustees), viii + 127 pp., pls. I-IX.

COPE, E. D.

1867. A review of the species of the Amblystomidae. *Proc. Acad. Nat. Sci. Phila.*, 1867, 166-211.

1889. The Batrachia of North America. *Bull. U. S. National Museum*, 32, 525 pp., 86 pls., 119 figs. in text.

DUNN, E. R.

1926. The salamanders of the family Plethodontidae (Northampton, Mass., Smith College), xi + 441 pp., 3 pls., 86 figs. in text.

1929. A new salamander from southern California. *Proc. U. S. National Museum*, 74, 1928 [1929], pp. 1-3.

GIRARD, C.

1856. On a new genus and species of Urodela, from the collections of the U. S. Expl. Exped. under Comm. Charles Wilkes, U.S.N. *Proc. Acad. Nat. Sci. Phila.*, 8, 140-141.

GRAY, J. E.

1850. Catalogue of the specimens of amphibia in the collection of the British Museum. Part II. Batrachia Gradientia, etc. (London, printed by order of the trustees), 72 pp., pls. 3, 4.

GRINNELL, J., and CAMP, C. L.

1917. A distributional list of the amphibians and reptiles of California. *Univ. Calif. Publ. Zool.*, 17, 127-208, 14 figs. (maps) in text.

KLAUBER, L. M.

1927. Notes on the salamanders of San Diego County, California. *Bull. Zool. Soc. of San Diego*, 3, 1-4.

LOCKINGTON, W. N.

1880. List of Californian reptiles and batrachia collected by Mr. Dunn and Mr. W. J. Fisher in 1876. *Am. Naturalist*, 14, 295-296.

RIDGWAY, R.

1912. Color standards and color nomenclature (Washington, D. C., published by the author), iii + 1-43 + 1 pp., pls. 1-53.

SLEVIN, J. R.

1928. The amphibians of western North America. *Occas. Papers, Calif. Acad. Sci.*, 16, 152 pp., 23 pls.

**STEPHENS, F.**

1921. An annotated list of the amphibians and reptiles of San Diego County, California. *Trans. San Diego Soc. Nat. Hist.*, 3, 57-69.

**STOREY, T. I.**

1925. A synopsis of the Amphibia of California. *Univ. Calif. Publ. Zool.*, 27, 1-342, pls. 1-18, 42 figs. in text.

**VAN DENBURGH, J.**

1916. Four species of salamanders new to the state of California, with a description of *Plethodon elongatus*, a new species, and notes on other salamanders. *Proc. Calif. Acad. Sci.*, ser. 4, 6, 215-221.

*Transmitted March 16, 1929.*

A NEW KANGAROO RAT FROM THE  
UPPER SACRAMENTO VALLEY,  
CALIFORNIA

BY

JOSEPH GRINNELL AND JEAN M. LINSDALE

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOOLOGY  
Volume 30, No. 17, pp. 453-459, 1 figure in text  
Issued June 15, 1929

UNIVERSITY OF CALIFORNIA PRESS  
BERKELEY, CALIFORNIA

---

CAMBRIDGE UNIVERSITY PRESS  
LONDON, ENGLAND

# A NEW KANGAROO RAT FROM THE UPPER SACRAMENTO VALLEY, CALIFORNIA

BY

JOSEPH GRINNELL AND JEAN M. LINSDALE

(Contribution from the University of California Museum of Vertebrate Zoology)

---

Field work in connection with a faunal survey being conducted under the auspices of the California Museum of Vertebrate Zoology along a cross-section of the mountain system in the Lassen Peak region has brought to light a well-marked race of *Dipodomys heermanni*. The existence of this race was unsuspected at the time of the senior author's revision of *Dipodomys* (Grinnell, 1922), although a few of the specimens referred to *D. h. eximius* in that report are now included within the scope of the new form. This new race may now be named and described as follows.

## *Dipodomys heermanni saxatilis*, new subspecies

Stony-ground Kangaroo Rat

*Type*.—Female adult, skin-and-skull; no. 34963, Mus. Vert. Zool.; mesa near Dale's, on north side of Paine's Creek, 700 feet altitude, Tehama County, California; December 27, 1924; collected by J. Grinnell; original no. 6192.

*Diagnosis*.—A four-toed, middle-sized, broad-faced kangaroo rat, with white-tipped tail, belonging to the *heermanni* group. In coloration, like *Dipodomys heermanni californicus* Merriam, but color tones throughout darker; white areas more restricted; blackish or dark areas more extended. Size throughout, decidedly smaller than in *californicus* or *heermanni*.

*Remarks*.—The blackish facial marking heavy, approaching nearest, among all the kangaroo rats of California, the condition in *morroensis*; ears blackish with but faint traces of the light markings, these represented only in gray. White spots above and behind eye and at base of ear, reduced as compared with their extent in *californicus*; light area between eye and nose reduced and overwashed with dusky; white side-stripes of tail decidedly narrower than in *californicus*; white at tip of tail much smaller in amount than in *californicus*; ventral dark tail-stripe and foot-sole-stripe blacker than in *californicus*; top of head and middle of dorsum, decidedly blackish; dilution of brown on sides, buffy toned rather than ochraceous as in *californicus*.

*With respect to size:* smaller than *californicus*, most appreciably so as regards ear and hind foot. Fourteen adult males from the type locality give average and extreme measurements in millimeters as follows: total length, 286.2 (260–310); tail vertebrae, 174.7 (152–190); hind foot, 42.9 (41–45); ear from crown, 12.6 (11–14); greatest length of skull, 37.0 (35.6–38.7); breadth of skull across bullae, 22.9 (22.1–23.5); spread of maxillary arches, 21.4 (20.2–23.3); greatest length of nasals, 13.6 (12.9–15.1); weight, in grams, 60.6 (53–70). Eleven adult females give figures similarly as follows: total length, 282.8 (271–300); tail vertebrae, 174.8 (165–188); hind foot, 41.5 (40–44); ear from crown, 12.5 (12–13); greatest length of skull, 36.9 (36.3–37.4); breadth of skull across bullae, 22.8 (22.1–23.4); spread of maxillary arches, 21.5 (20.8–22.2); greatest length of nasals, 13.8 (13.4–14.2); weight (five of the eleven were pregnant), in grams, 58.8 (53–63.5). In most respects the two sexes are here shown to be alike; at best, males exceed females in size by but a small percentage.

*As to skull:* general size smaller than in *californicus*, this reflected in all dimensions (see measurements above and in Grinnell, 1922, pp. 36, 40); angle formed by lateral profile of rostrum with outstanding anterior profile of maxillary portion of zygomatic arch more obvious, in other words, not so shallow; to express the condition in another way, face less tapering anteriorwards—outline of skull in dorsal view, “squarer.”

The subspecies *Dipodomys heermanni eximius*, another occupant of the Sacramento River drainage basin, was described (Grinnell, 1919, p. 205) from the Marysville Buttes in Sutter County. One of its characters also, as compared with *D. h. californicus*, was that of small size. But its other character was relative pallor of coloration, with restriction of dark markings and extension of white. As compared with the topotype series of *eximius*, the new form is strikingly darker in color, the contrast in coloration being greater than with *californicus*.

In the senior author's revision (1922, p. 42), certain specimens from the western foothills of the northern Sierra Nevada were placed under the name *eximius*; but comment was made as to slight differences shown by them. Of these, we now are of opinion that the ones available to us, from Limekiln, Eldorado County, and near Chico, Butte County, should be removed from *eximius* and placed with *saxatilis*. By this action a range for *saxatilis* is indicated south from the type locality of the latter to Eldorado County, as shown in the accompanying map (fig. 1). Also, certain other specimens, from the vicinity of Red Bluff, recorded under *eximius*, all from the west side of the Sacramento River, now appear best referred to *californicus*. The name *eximius* is thus left restricted, so far as the material now in hand is concerned, to the Marysville Buttes, a not unreasonable procedure when it is recalled to mind that this elevated land mass is far isolated by the Sacramento River channel on the west and the Feather River channel on the east, which join at the south, and by the inundatable lowlands extending between the Feather and Sacramento rivers to the north of the Buttes. The population of

kangaroo rats thus segregated in the middle of the Sacramento Valley may be held to have been kept, for a long period, uninfluenced by interbreeding with either of the races (*californicus* and *saxatilis*) inhabiting the two foothill margins of the Sacramento Valley.

To repeat, the race we now newly name is distinguished from *californicus* in practice by its small size, from *eximius* by its dark coloration.

*Distribution.*—The following localities for *saxatilis* are represented in the material before us, all of this contained in the Museum of Vertebrate Zoology. Tehama County: vicinity of Dale's, 600 to 700 feet altitude, 34 specimens; eleven miles southeast of Red Bluff, 300 feet, east of Sacramento River, 5; two and one-half miles east-northeast of Tehama, 300 feet, 8. Butte County: Butte Creek, four miles southeast of Chico, 450 feet, 4; eight miles southeast of Chico, 450 feet, 14. Eldorado County: Limekiln, 1200 feet, 3. Total specimens examined, 68. The range of this race thus lies entirely to the eastward of the Sacramento River, and on rising ground, though at low altitudes, from the south side of Battle Creek, Tehama County, south nearly to the South Fork of the American River. (See map, fig. 1.)

After drawing up the foregoing diagnosis we found opportunity to go into the field for the purpose of obtaining more material, both specimens and facts of distribution, that would bear upon the question of kangaroo rat populations on the east side of the Sacramento Valley. The week, January 1 to 7, 1929, was spent in this way in the territory between Placerville, Eldorado County, and Red Bluff, Tehama County. The results of this trip both confirmed and extended our inferences based upon previously available information.

Trapping for kangaroo rats and questioning of persons who live in the region showed that the rats are present, but probably not continuously and surely not numerous, in the foothills east from the Sacramento Valley. By the same means we found the animals to be present in colonies in places just above and east of the edge of the flat valley floor. The chief requirement for sites for these colonies appeared to be soil of such consistency and slope that it would remain well drained through the wet winter months. Conversely, close examination at many places showed no evidence of the presence of kangaroo rats on any of the flat ground in the floor of the Sacramento Valley. Even in the winter of 1928-29, an especially dry one, the valley soils were, we judged, too water-logged for any kangaroo rats to live on them. Persons to whom we talked who were familiar with these animals as occurring on Marysville Buttes (territory occupied by the race *eximius*) and above the eastern edge of the valley (occupied by *saxatilis*) had never known of an occurrence of the rats on the main floor of the valley.



Specimens we obtained at points farther north verified the conclusion that the Sacramento River plus its valley floor keeps the kangaroo rat populations separated and distinctly different on the east and west sides at least as far north as Red Bluff.

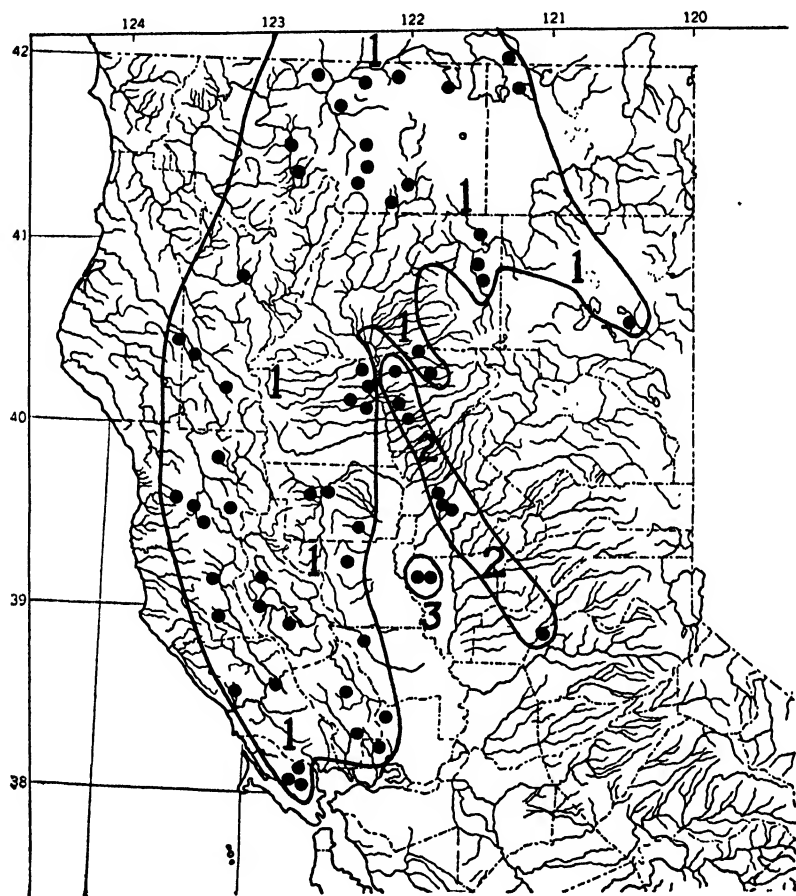


Fig. 1. Map showing occurrence of kangaroo rats of the *Dipodomys heermanni* group in northern California. Subspecies: 1, *D. h. californicus*; 2, *D. h. saxatilis*; 3, *D. h. eximius*. Spots show location of places whence specimens have been examined.

In the present connection it naturally became necessary to look into the status of the lately named *Dipodomys heermanni gabrielsoni* Goldman (1925, pp. 33-34), with type locality, Brownsboro, Jackson County, Oregon. Through the courtesy of the United States Biological Survey we have before us four topotypes of *gabrielsoni*, part of the series upon which this name was based and therefore assumably showing adequately the characters of the subspecies represented.

To give our conclusion at once, we fail to find any ground for recognizing *gabrielsoni*; in our judgment the name *gabrielsoni* falls into the synonymy of *californicus*.

Just four characters are cited by Goldman to distinguish *gabrielsoni* from *californicus*: (1) color darker, (2) maxillary arches broader, (3) skull relatively narrower posteriorly, (4) mastoid bullae smaller.

As to coloration, it is true that *gabrielsoni* (June and July taken examples) is slightly the darker-toned as compared with topotypes of *californicus*, from Ukiah, Mendocino County, California (November taken); but it is to us indistinguishable in minutest detail of color from topotypes of *Dipodomys californicus trinitatis* Kellogg (1916, p. 366), from Helena, Trinity County, California (February taken), as also from other locality representations (summer taken) from northwestern California. The earlier described race *trinitatis*, it will be recalled, was considered by Grinnell (1922, p. 38) as not warranting recognition, for the reason that the characters cited for it were of no more importance than other characters that are apparent from place to place in the general range of *californicus*.

As to width of maxillary arch, and its postero-lateral angulation, we are able to see this in more than ordinary degree for *californicus* in but two out of the four skulls of *gabrielsoni* at hand. One of these does, indeed, show greater width in this respect than any skull examined of *californicus*. An average greater width of maxillary arch doubtless does obtain in the entire topotype series.

As to size of mastoid bullae and width of skull posteriorly, these two features obviously are closely correlated. In neither can we see the faintest peculiarity of the Brownsboro specimens as compared with our Trinity and Siskiyou county specimens or others from elsewhere in northwestern California.

Now granting a possible tendency toward darkening of coloration in the Brownsboro series, as also an average greater width of maxillary arch, are these tendencies of sufficient scope to justify cutting off a population of the *californicus* type of kangaroo rat under separate nomenclature? We think not; for "*gabrielsoni*" is exceedingly similar to "*trinitatis*," previously named. If separation be made now, then, judging from the rather abundant material before us, the line of geographic demarcation would have to be drawn somewhere south of our Trinity County localities, and the northern form thus set apart be designated as *trinitatis*. But if these local tendencies be

recognized in nomenclature, then, as already pointed out (Grinnell, *loc. cit.*, p. 38), a Marin County race, at the south, would have to be named; also the name *pallidulus* Bangs would have to be resuscitated to indicate a tendency to pallor in animals from certain interior valleys. And what territory would then be left for *californicus* proper?

In other words, the only practicable course of systematic procedure, on the evidence presented by Goldman and as before us in the shape of series of specimens, is to include *gabrielsoni* along with the rest of such incipencies, and to use the name *californicus* to cover all the kangaroo rats of the Coast Range territory from the north side of San Francisco Bay north to and including the Rogue River Valley of southern Oregon.

One more criticism should be levied here and, we hope, accepted without any implication of animus. Goldman says at the outset of his description of *gabrielsoni* (1925, p. 33): "In northern California and southern Oregon *Dipodomys heermanni* has hitherto been known to occur only on the eastern side of the Cascade Mountains." Since no hint is given as to what meaning is intended by the uncertain term "Cascade Mountains," it is difficult to understand this statement. If it was meant to say that in this region no kangaroo rats had been captured on ground which drains directly to the Pacific on the westward, then the assertion is surely misleading. For not only did Miss Kellogg (1916, p. 367) record a large series from the valley of Scott River, a tributary of the Klamath, but Grinnell (1922, p. 41) recorded *californicus* from at least ten localities in northern California west of the longitude of Mount Shasta, and hence positively on the Pacific drainage slope. Also, it is noteworthy that *gabrielsoni* was named from a locality only thirty miles air-line north of the California-Oregon boundary, and less than forty miles from Hornbrook, Siskiyou County, whence the Biological Survey, itself, has specimens of *californicus*!

A suggestively close parallel is afforded by the *Thomomys bottae* group of pocket gophers in northwestern California and southern Oregon. Vernon Bailey (1915, p. 48), while commenting freely upon the many local variations apparent in series of specimens from numerous localities extending from the Rogue River Valley, Oregon, south to Petaluma, Sonoma County, California, includes all these minor differentiates under the one subspecific name, *Thomomys bottae leucodon* Merriam, which was based upon specimens from Grants Pass, Oregon.

## LITERATURE CITED

BAILEY, V.

1915. Revision of the pocket gophers of the genus *Thomomys*. U. S. Dept. Agr., N. Am. Fauna, 39, 136 pp., 8 pls., 10 figs. in text.

GOLDMAN, E. A.

1925. A new kangaroo rat of the genus *Dipodomys* from Oregon. Proc. Biol. Soc. Wash., 38, 33-34.

GRINNELL, J.

1919. Four new kangaroo rats from west-central California. Proc. Biol. Soc. Wash., 32, 203-205.
1922. A geographical study of the kangaroo rats of California. Univ. Calif. Publ. Zool., 24, 1-124, pls. 1-7, 24 figs. in text.

KELLOGG, L.

1916. Report upon mammals and birds found in portions of Trinity, Siskiyou and Shasta counties, California, with description of a new *Dipodomys*. Univ. Calif. Publ. Zool., 12, 335-398, pls. 15-18.

*Transmitted March 20, 1929.*



# INDEX

University of California Publications in Zoology, Volume 30.  
**Titles of papers and new systematic names are in boldface.**

## **A New Kangaroo Rat from the Upper Sacramento Valley, California, 453-459.**

- Accipiter velox*, 104.  
 Acknowledgments, 51, 52, 163, 177, 231, 301, 393, 428.  
*Actitis macularia*, 72.  
 Alaska Collared Lemming, 424.  
*Alces gigas*, 151.  
*Alopex lagopus innuitus*, 421.  
**American Badger (*Taxidea taxus*), The Muscular Anatomy of, 205-219.**  
*Anas platyrhynchos*, 64.  
*Aneides lugubris*, 450.  
*Anthus rubescens*, 141.  
*Aphriza virgata*, 73.  
*Aquila chrysaetos*, 111.  
*Archibuteo*, 199.  
 Arctic Least Weasel, 421.  
*A (rectomys). kennicottii*, 423.  
*Asio flammeus*, 199.  
*Astur atricapillus atricapillus*, 104.  
*Asyndesmus lewisii*, 429.  
 Atlin, description of, 54; region, zonal and faunal position of, 56; check list of birds of, 59; check list of mammals of, 145.  
**Atlin Region, Northern British Columbia, Report on a Collection of Birds and Mammals from, 51-162.**  
*Baeolophus*, measurements of, 165; map showing distribution of, 167.  
*inornatus affabilis*, 164, 166.  
*cineraceus*, 168.  
*griseus*, 168.  
*inornatus*, 164, 166.  
*murinus*, 164, 166.  
*sequestratus*, 166.  
*Balanosphyra formicivora bairdi*, 429.  
**Bassariscus astutus, Systematic Notes on the Subspecies of, with Description of One New Form from California, 39-50.**  
*Bassariscus*, 39.  
*astutus astutus*, type locality, 46.  
*flavus*, 39, 45; type locality, 46.  
*insulicola*, type locality, 46.  
*nevadensis*, 39, 45; type locality, 46.  
*octavus*, diagnosis of, 39; measurements, 40; type locality, 46.

- oregonus*, 44.  
*palmaris*, 39, 45; type locality, 46.  
*raptor*, 39; measurements, 40; type locality, designation by restriction, 44, 46.  
*saxicola*, 39; type locality, 46.  
*Batrachoseps attenuatus*, 450.  
 Bear, Black, 232; Blue, 234; Cinnamon, 232; Kermode, 233; white, 233.  
**Bears, Records of Supernumerary teeth in, 243.**  
 Beaver, 149.  
 Birds, skulls of, 315.  
**Black Bear, from Vancouver Island, British Columbia, A New Race of, with Remarks on Other Northwest Coast Forms of *Euarctos*, 231-242.**  
 Blackbird, Rusty, 120.  
 Bluebird, Mountain, 145.  
*Bombycilla garrula pallidiceps*, 133.  
*Bonasa umbellus umbelloides*, 85.  
*Branta canadensis*, 68.  
**Brower, Charles D., Mammals Collected by, at Point Barrow, Alaska, 419-425.**  
*Bubo virginianus lagophonus*, 113.  
*subarcticus*, 113.  
 Buena Vista Lake, outbreak of house mice in dry bed of, 189.  
 Buffle-head, 67.  
 Burt, W. H., 427-442.  
 Bush-tit, Black-tailed, 169.  
*Buteo*, 199.  
*borealis calurus*, 199.  
*harlani*, 104.  
*Calcarius lapponicus alasceus*, 121.  
 California, one new form of *Bassariscus* from, 39-50.  
*Canachites canadensis osgoodi*, 84.  
*Canis leste*, 147.  
 Carceross, description of, 54.  
*Carpodacus purpureus purpureus*, 120.  
*Castor canadensis canadensis*, 149.  
*Centurus carolinus*, 429.  
*uropygialis uropygialis*, 429.  
*Ceophloeus pileatus picinus*, 429.  
*pileatus*, 429; feather tracts of, 431, 432.  
*Cerchneis sparveria sparveria*, 113.  
*Ceryle alcyon caurina*, 115.

# Index

- Chamaea**, map showing distribution of, 173.  
*fasciata canicauda*, 169.  
     *henshawi*, 171.  
     *intermedia*, 171.  
     *phaea*, 171.  
     *rufula*, 171.  
**Charadrius semipalmatus**, 72.  
**Charitonetta albeola**, 67.  
**Chickadee**, Columbian, 142; Long-tailed, 142; San Pedro Martir Mountain, 163; Short-tailed, 142.  
**Chipmunk**, Gray-headed, 149.  
**Chordeiles virginianus virginianus**, 116.  
**Circus hudsonius**, 104, 199.  
**Citellus plesius plesius**, 148.  
     *parryi kennicottii*, 423.  
**Colaptes auratus auratus**, 429.  
     *borealis*, 115.  
     *luteus*, 429; feather tracts of, 438; embryos of, drawings of, 440.  
     *cafer collaris*, 429.  
**Collared Lemming**, Alaska, 424.  
**Coloration**, adventitious, of Logger-head Shrike, 401.  
**Colymbus auritus**, 61.  
     *holboellii*, 61.  
**Corvus corax principalis**, 120.  
     *sinuatus*, 200.  
**Coyote**, Northern, 147.  
**Crossbill**, White-winged, 120.  
**Curlew**, Hudsonian, 72.  
**Dafla acuta tzitzihua**, 65.  
**Dendragapus**, map showing distribution, 74.  
     *fuliginosus fuliginosus*, tails figured, 82.  
         *howardi*, tails figured, 82.  
         *sierrae*, tails figured, 82.  
         *sitkensis*, tails figured, 81.  
     *obscurus flemingi*, 73; tails figured, 75.  
     *obscurus*, tails figured, 79.  
     *richardsonii*, tails figured, 77.  
**Dendroica aestiva aestiva**, 138.  
     *coronata hooveri*, 139.  
     *striata*, 139.  
     *townsendi*, 140.  
**Dicrostonyx rubricatus rubricatus**, 424.  
**Dipodomys**, 198.  
     *heermanni*, map showing occurrence of in northern California, 456.  
     *californicus*, 453.  
     *trinitatis*, 457.  
     *eximius*, 454.  
     *gabrielsoni*, 456.  
     *saxatilis*, 453.  
**Dixon, J.**, cited, 1.  
**Dryobates borealis**, 430.  
     *nuttallii*, 430.  
     *pubescens medianus*, 430.  
     *nelsoni*, 115.  
     *turati*, 430.  
     *scalaris cactophilus*, 430.  
     *villosus orius*, 430.  
         *leucomelas*, 115.  
         *villosus*, 429.  
**Duck**, Lesser Scaup, 65.  
     Western Harlequin, 67.  
**Eagle**, Golden, 111; Northern Bald, 111.  
**Empidonax hammondii**, 118.  
     *traillii alnorum*, 118.  
     *wrightii*, 118.  
**Ensatina**, in California, Notes on the Genus, with Description of a New Species from the Sierra Nevada, 443-452.  
**Ensatina croceater**, 443, 445; measurements, 446.  
     *eschscholtzii*, 443, 449, 450.  
     *klauberi*, 443.  
     *oregonensis*, 450.  
     *platensis*, 443.  
     *sierrae*, 448.  
**Erethizon epixanthum nigrescens**, 151.  
**Ereuntes pusillus**, 70.  
**Euaetios**, northwest coast forms of, remarks on, 231.  
**Euphagus carolinus**, 120.  
**Eutamias minimus caniceps**, 149.  
**Falco columbarius suckleyi**, 112.  
     *peregrinus anatum*, 112.  
     *rusticolus rusticolus*, 111.  
     *sparverius phalaena*, 199.  
**Feather tracts**, classification of, 429; of *Ceophloeus pileatus pileatus*, 431.  
**Finch**, Eastern Purple, 120.  
**Fisher, Edna M.**, 221-229.  
**Flicker**, Boreal, 115.  
**Flycatcher**, Alder, 118; Hammond, 118; Olive-sided, 118; Wright, 118.  
**Fox**, Arctic, 421; British Columbia Red, 147; Red, 421.  
**Fox Sparrow** (*Passerella iliaca*), Variations in the, with Reference to Natural History and Osteology, 251-392.  
**Fox Sparrow**, variations in internal structure in the, 309; seasonal variation in weight, 311; geographic variation in weight, 313.  
**Gallinaria delicata**, 69.  
**Garter snakes**. See Snakes, garter.  
**Gavia**, immer, 62.  
     *pacifica*, 62.  
     *stellata*, 62.

# Index

- Geothlypis trichas occidentalis*, 140.  
*Gignoux, C.*, cited, 189.  
*Glaucionetta islandica*, 66.  
 Golden-eye, Barrow, 66.  
 Gopher, Pocket, Honey Lake, 2;  
     Sickle-toothed, 180; Solitary, 177.  
**Gophers, Pocket, from Western Nevada, A Systematic Study of Some, 177-188.**  
 Goose, Canada, 68.  
 Goshawk, Eastern, 104.  
 Grebe, Holboell, 61; Horned, 61.  
 Grinnell, Hilda Wood, cited, 1.  
 Grinnell, J., 1-6, 163-175, 177-188, 453-459.  
 Ground Squirrel, Bennett, 148; Kennicott, 423.  
 Grouse, Alaska Spruce, 84; Fleming, 73; Gray Ruffed, 85.  
 Gull, Bonaparte, 63; Herring, 62; Short-billed, 62.  
*Gulo luscus*, 147.  
 Gyrfalcon, Gray, 111.  
*Haliaeetus leucocephalus alascanus*, 111.  
 Hall, E. R., 7-38, 39-50, 189-203, 205-219, 231-242, 243-250, 419-425.  
 Hare, Mackenzie Varying, 151.  
 Hawk, Black Pigeon, 112; Desert Sparrow, 199; Duck, 112; Harlan, 105; Marsh, 104, 199; Rough-legged, 199; Sharp-shinned, 104; Sparrow, 113; Western Red-tailed, 199.  
*Heterosceus incanus*, 72.  
*Hirundo erythrogaster*, 132.  
*Histrionicus histrionicus pacificus*, 67.  
 Hoary Marmot, Northern, 422.  
 Holboell Grebe, 61.  
 Honey Lake Pocket Gopher, 2.  
**Honey Lake Valley, The Pocket Gopher of, 1-6.**  
 Horned Grebe, 61.  
**House Mice, in Kern County, California, An Outbreak of, 189-203.**  
 House mice, time of outbreak in Kern County, California, 190; source of outbreak, 190; numbers of in outbreak, 192; economic bearings of outbreak, 194; biological inferences: natural selection, operation at an accelerated rate, 196; radial migration of, 197; relation of predatory birds to, 199; relation of predatory mammals to, 200; causes of over-abundance of population of, 203.  
 Hummingbird, Rufous, 116.  
*Hylocichla guttata guttata*, 144.  
     *pallasi*, 144.  
     *ustulata swainsoni*, 143.  
 Insular forms, criterion for the treatment of, 46.  
 Internal structure in the Fox Sparrow, variations in, 309.  
*Iridoprocne bicolor*, 133.  
*Ixoreus naevius meruloides*, 145.  
 Jaeger, Parasitic, 62.  
 Jay, Canada, 120.  
 Junco, Cassiar, 131.  
*Junco hyemalis connectens*, 131.  
**Kangaroo Rat, A New, from the Upper Sacramento Valley, California, 453-459.**  
 Kangaroo Rat, Stony-ground, 453.  
 Kennicott Ground Squirrel, 423.  
 Killdeer, 72.  
 Kinglet, Ruby-crowned, 143.  
     Western Golden-crowned, 143.  
*Lagopus lagopus alascanus*, 87; bill figured, 89.  
     *albus*, 86; bill figured, 89.  
     *alexandrae*, bill figured, 89.  
     *ungavus*, bill figured, 89.  
     *leucurus leucurus*, 103.  
     *rupestris*, map showing distribution of subspecies of, 97.  
     *dixonii*, 97.  
     *kelloggii*, 97.  
     *rupestris*, 94.  
*Lanius borealis*, 134.  
     *ludovicianus excubitorides*, first fall molt of, 405.  
     *gambeli*, views of right wing, 397; molt, first fall of, 404.  
**Lanius ludovicianus Linnaeus, Loggerhead Shrike, The Molts of the, 393-417.**  
 Lark, Pallid Horned, 119.  
*Larus argentatus*, 62.  
     *brachyrhynchus*, 62.  
     *philadelphia*, 63.  
 Least Weasel, Arctic, 421.  
 Lemming, Alaska Collared, 424; Point Barrow, 423.  
*Lemmus alascanus*, 423.  
*Lepus americanus macfarlandi*, 151.  
 Linsdale, J., 251-392, 453-459.  
 Literature cited: Muscular anatomy of Mephitis, Spilogale, and Martes, 38; *Bassariscus astutus*, 47; Birds and mammals from Atlin region, British Columbia, 152; New subspecies of birds from the Pacific coast of North America, 175; Pocket gophers from western Nevada, 183; Garter snakes, 229; New Black Bear, 237; Variations in Fox Sparrow (*Passerella iliaca*), 377; Molts of Loggerhead Shrike, 417; Mammals collected by Charles D. Brower, 423; Pterylography of certain North American wood-



# Index

- peckers, 442; Genus *Ensatina* in California, 451; New Kangaroo Rat from upper Sacramento Valley, 459.
- Lobipes lobatus*, 69.
- Loggerhead Shrike, molts of the, 393-417; pterylography of wing, 396; juvenal plumage, 399; adventitious coloration, 401.
- Longspur, Alaska, 121.
- Loon, Common, 62; Pacific, 62; Red-throated, 62.
- Lophodytes cucullatus*, 64.
- Lower California, ring-tailed cats of, 45.
- Loxia leucoptera*, 120.
- Magpie, American, 119.
- Mallard, 64.
- Mammals Collected by Charles D. Brower at Point Barrow, Alaska, 419-425.**
- Marila affinis*, 65.
- Marmot, Hoary, 148; Northern Hoary, 422.
- Marmota caligata caligata*, 148, 422.
- Martes, differences from *Mephitis* and *Spilogale* in musculature, 37; flexor carpi ulnaris of, 215; tibialis posterior, flexor hallucis longus, and flexor digitorum longus of, 218.
- Martes caurina humboldtensis*, myology of, 8, 30.
- Melanerpes erythrocephalus*, 429.
- Melospiza lincolni lincolni*, 132.
- Mephitis*, differences from *Spilogale* and *Martes* in musculature, 37; flexor carpi ulnaris of, 215; tibialis posterior, flexor hallucis longus, and flexor digitorum longus of, 218.
- Mephitis occidentalis*, myology of, 8, 30.
- Merganser, American, 64; Hooded, 64; Red-breasted, 64.
- Mergus americanus*, 64.
- serrator, 64.
- Microtus californicus*, 192.
- drummondii, 150.
- mordax mordax, 150.
- operarius endoeus, 424.
- Miller, A. H., 393-417.
- Molt, first fall, of Loggerhead Shrike, 402, 404, 405; prenuptial, 409; second fall, 410.
- Molts of the Loggerhead Shrike, *Lanius ludovicianus* Linnaeus, The, 393-417.**
- Moose, Alaska, 151.
- Mountain Chickadee, San Pedro Martir, 163.
- Mouse, Cantankerous Meadow, 150; Dall Lemming, 150; Drummond Meadow, 150; Northern White-footed, 149, 198; Pocket, 198; House, 201.
- Mus musculus*, outbreak of in Kern County, California. See House mice.
- Muscular Anatomy of the American Badger (*Taxidea taxus*), The 205-219.**
- Muscular Anatomy of Three Mustelid Mammals, *Mephitis*, *Spilogale*, and *Martes*, The, 7-38.**
- Muskrat, Northwestern, 150.
- Mustela arctica*, 420.
- cicognanii richardsonii, 147.
- rixosa eskimo, 421.
- Mustelid Mammals, Three, *Mephitis*, *Spilogale*, and *Martes*, Muscular Anatomy of, 7-38.**
- Myadestes townsendi*, 143.
- Myiochanes richardsonii richardsonii*, 118.
- Neosorex navigator navigator*, 146.
- Neotoma cinerea saxamans*, 150.
- Nettion carolinense*, 65.
- Nevada, Western, Pocket Gophers from, A Systematic Study of Some, 177-188.**
- New Race of Black Bear from Vancouver Island, British Columbia, with Remarks on other Northwest Coast Forms of *Euarctos*, 231-242.**
- New Subspecies of Birds (*Penthestes*, *Baeolophus*, *Psaltiriparus*, *Chamaea*) from the Pacific Coast of North America, 163-175.**
- Nighthawk, Eastern, 116.
- North American Woodpeckers, Certain, Pterylography of, 427-442.**
- Northern Hoary Marmot, 422.
- Northern Tundra Vole, 424.
- Notes on the Genus *Ensatina* in California, with Description of a New Species from the Sierra Nevada, 443-452.**
- Numenius hudsonicus, 72.
- Nuthatch, Red-breasted, 142.
- Nuttallornis borealis*, 118.
- Oidemia deglandi dixonii*, 67.
- perspicillata, 68.
- Ondatra zibethica spatulata*, 150.
- Osprey, 113.
- Otocoris alpestris arcticola*, 119.
- Otter Creek, description of, 56.
- Outbreak of House Mice in Kern County, California, An, 189-203.**
- Owl, Arctic Horned, 113; Barn, 199; Hawk, 114; Ruddy Horned, 113; Short-eared, 199.

## Index

- Oxyechus vociferus*, 72.  
**Pacific Coast of North America, New Subspecies of Birds** (*Penthestes*, *Baeolophus*, *Psaltriparus*, *Chamaea*), from the, 163-175.  
*Pandion haliaeetus carolinensis*, 113.  
*Passerculus sandwichensis alaudinus*, 121.  
*Passerella*, comparison with *Melospiza*, 363.  
***Passerella iliaca*, Variations in, with Reference to History and Osteology**, 251-392.  
*Passerella iliaca*, natural history of, 267.  
     *cancscens*, skeleton of, illustrated, 306.  
*Penthestes atricapillus*, 164.  
     *septentrionalis*, 142.  
     *gambeli abbreviatus*, 142.  
     *atratus*, 163.  
     *baileyae*, 163.  
     *hudsonicus columbianus*, 142.  
***Penthestes*, *Baeolophus*, *Psaltriparus*, *Chamaea*, New Subspecies of, from the Pacific Coast of North America**, 163-175.  
*Perisoreus canadensis canadensis*, 120.  
*Peromyscus*, 198.  
     *maniculatus borealis*, 149.  
*Petrochelidon lunifrons lunifrons*, 132.  
 Pewee, Western Wood, 118.  
*Phalaropus*, Northern, 69.  
*Phoebe*, Northern Say, 116.  
*Pica pica hudsonia*, 119.  
*Picoides americanus americanus*, 430.  
     *fasciatus*, 115.  
*Pintail*, American, 65.  
*Pipit*, 141.  
*Pisobia bairdii*, 69.  
     *maculata*, 69.  
     *minutilla*, 70.  
*Plain Titmouse*, Oregon, 166; San Pedro Martir, 164.  
*Plain Titmouses*, map showing distribution of, 167.  
*Planesticus migratorius migratorius*, 144.  
*Plethodon croceator*, 444.  
*Plover*, Semipalmated, 72.  
*Plumage*, juvenal, of Loggerhead Shrike, 399; first winter, 407.  
*Pocket Gopher*, Honey Lake, 2; Sickie-toothed, 180; Solitary, 177.  
***Pocket Gopher*, The, of Honey Lake Valley**, 1-6.  
*Pocket mice*, 198.  
**Point Barrow, Alaska, Mammals Collected by Charles D. Brower at**, 419-425.  
*Point Barrow Lemming*, 423.  
*Porcupine*, Dusky, 151.  
*Potos flavus*, 7.  
 Predatory birds, mammals, 200.  
*Perognathus*, 198.  
*Psaltriparus minimus californicus*, 169.  
     *melanurus*, 169.  
     *minimus*, 169.  
     *plumbeus*, 169.  
*Ptarmigan*, Alaska Willow, 87; Gray Rock, 90; Southern Willow, 86; White-tailed, 103.  
*Pterylography* of wing of Loggerhead Shrike, 396.  
***Pterylography* of Certain North American Woodpeckers**, 427-442.  
*Rat*, Kangaroo, 198; Stony-ground, 453.  
*Rat*, Wood, Northern Bushy-tailed, 150.  
*Raven*, Northern, 120.  
*Ravens*, 200.  
*Redstart*, American, 141.  
*Regulus calendula calendula*, 143.  
     *satrappa olivaceus*, 143.  
**Report on a Collection of Birds and Mammals from the Atlin Region, Northern British Columbia**, 51-162.  
*Ring-tailed cats*, of Lower California, 45.  
*Riparia riparia*, 133.  
*Robin*, Eastern, 144.  
**Sacramento Valley, Upper, California, A New Kangaroo Rat from**, 453.  
*Saddle-backed Shrew*, Tundra, 419.  
*Salamander*, Sierra Nevada, 448.  
*San Pedro Martir*, Mountain Chickadee, 163; Plain Titmouse, 164.  
*Sandpiper*, Baird, 69; Least, 70; Pectoral, 69; Semipalmated, 70; Solitary, 70; Spotted, 72.  
*Sayornis sayus yukonensis*, 116.  
*Seiurus hudsonicus hudsonicus*, 149.  
*Scoter*, Dixon White winged, 67; Surf, 68.  
*Seiurus noveboracensis notabilis*, 140.  
*Selasphorus rufus*, 116.  
*Setophaga ruticilla*, 141.  
*Shoveller*, 65.  
*Shrew*, Dusky, 146; Masked, 146; Tundra Saddle-backed, 419; Water, 146.  
**Shrike, Loggerhead, *Lanius ludovicianus* Linnaeus, The Molts of the**, 393-417.  
*Sialia currucoides*, 145.  
*Sierra Nevada*, description of a new species of *Ensatina* from, 443.  
*Sierra Nevada Salamander*, 448.  
*Siskin*, Pine, 121.  
*Sitta canadensis*, 142.  
*Skulls*, of birds, 315.

## Index

- Snakes, garter, supralabial and infra-labial formulae of young, 223.  
**Snakes, Pacific Garter, Variation within a Brood of**, 221-229.  
 Snipe, Wilson, 69.  
 Solitaire, Townsend, 143.  
 Sorex obscurus obscurus, 146.  
     personatus personatus, 146.  
     tundrensis, 419.  
 Sparrow, Eastern Chipping, 130;  
     Gambel White-crowned, 121;  
     Golden-crowned, 124, young, fig-  
     ured, opp. p. 51; Lincoln, 132;  
     Timber-line, 130; Western Savan-  
     nah, 121; Western Tree, 129.  
 Spatula clypeata, 65.  
 Spermophilus barrowensis, 423.  
 Sperry, C. C., cited, 283.  
 Sphyrapicus ruber ruber, 429; feather  
     tracts of, 436.  
     thyroideus thyroideus, 429.  
     varius nuchalis, 429.  
     varius, 429.  
 Spilogale, differences from Mephitis,  
     in musculature, 37; tibialis pos-  
     terior, flexor hallucis longus, and  
     flexor digitorum longus of, 218.  
 Spilogale phenax phenax, myology  
     of, 8, 30.  
 Spinus pinus, 121.  
 Spizella monticola ochracea, 129.  
     passerina passerina, 130.  
     taverneri, 130.  
 Squirrel, Bennett Ground, 148; North-  
     ern Red, 149; Kennicott Ground,  
     423.  
 Stercorarius parasiticus, 62.  
 Sterna paradisaea, 64.  
 Stony-ground Kangaroo Rat, 453.  
 Storer, T. I., 443-452.  
**Supernumerary Teeth, Records of in  
 Bears**, 243.  
 Surf-bird, 73.  
 Surnia ulula caparoch, 114.  
 Swallow, Bank, 133; Barn, 132; Cliff,  
     132; Northern Violet-green, 133;  
     Tree, 133.  
 Swarth, H. S., 51-162, 163-175; cited,  
     259.  
 Synaptomys borealis dalli, 150.  
**Systematic Notes on the Subspecies  
 of Bassariscus astutus, with De-  
 scription of One New Form from  
 California**, 39-50.  
**Systematic Study of Some Pocket  
 Gophers from Western Nevada**,  
 177-188.  
 Tachycineta thalassina, 133.  
 Tattler, Wandering, 72.  
 Taxidea taxus, muscular anatomy of,  
     205-219; view of muscles, 210-  
     211, note on humerus of, 212.  
 Teal, Green-winged, 65.  
**Teeth, Supernumerary, Records of, in  
 Bears**, 243.  
 Tern, Arctic, 64.  
 Thamnopsis sirtalis concinnus, 221.  
     infernalis, 221.  
     parietalis, 221.  
 Thomomys, 177.  
     bottae, 458.  
     bridgeri, 182.  
     falcifer, 180, 181; measurements,  
         180.  
     perpallidus aureus, 178.  
         canus, 2, 178.  
         perpes, 178, 179.  
     quadratus, 181.  
         fisheri, 181.  
         quadratus, 181.  
     relictus, 2; measurements, 3.  
     scapterus, 179.  
     solitarius, 177; measurements, 178.  
     townsendii nevadensis, 4, 181.  
     uinta, 182.  
 Thrush, Alaska Hermit, 144; Eastern  
     Hermit, 144; Northern Varied,  
     145; Olive backed, 143.  
 Titmouse, Oregon Plain, 166; San  
     Pedro Martir Plain, 164.  
 Titmouses, Plain, map showing dis-  
     tribution of, 167.  
 Totanus flavipes, 70.  
 Tringa solitaria, 70.  
 Tundra Saddle-backed Shrew, 419.  
 Tundra Vole, Northern, 424.  
 Tundra Weasel, 420.  
 Tyto pratincola, 199.  
 Ursus americanus, color phases, 236.  
     altifrontalis, 232, 235.  
     americanus, 232.  
     carlottae, 235.  
     cinnamomum, 232.  
     emmonsii, 233, 234, 235.  
     kermodei, 233, 234, 235.  
     perniger, 235.  
     pugnax, 234, 235.  
     vancouveri, 232, 235.  
**Variations in the Fox Sparrow (Pas-  
 serella iliaca) with Reference to  
 Natural History and Osteology**,  
 251-392.  
 Variation in internal structure of  
 Fox Sparrow, 309; studies in,  
 251; need for, 253; previous,  
 254; in weight: seasonal, 311,  
 individual, 312, geographic, 313.  
**Variation within a Brood of Pacific  
 Garter Snakes**, 221-229.  
 Vermivora celata celata, 136.  
     orestera, 136.  
     peregrina, 138.  
 Vireo, Western Warbling, 136.  
 Vireosylva gilva swainsonii, 136.  
 Vole, Northern Tundra, 424.

## Index

- Vulpes alascensis abietorum*, 147.  
*fulva alascensis*, 421.  
**Warbler**, Alaska Myrtle, 139; Black-poll, 139; Eastern Yellow, 138; Orange-crowned, 136; Pileolated, 141; Rocky Mountain Orange-crowned, 136; Tennessee, 138; Townsend, 140.  
**Water-thrush**, Grinnell, 140.  
**Waxwing**, Bohemian, 133.  
**Weasel**, Arctic Least, 421; Richardson, 147; Tundra, 420.  
*Wilsonia pusilla pileolata*, 141.  
**Wing**, pterylography of, of Logger-head Shrike, 396.  
**Wings**, of birds, literature on the, 428.  
**Wolverene**, 147.  
**Woodpecker**, Alaska Three toed, 115; Nelson Downy, 115; Northern Hairy, 115.  
**Woodpeckers**, North American, **Pterylography of Certain**, 427-442.  
**Wren-tit**, San Pedro Martir, 169.  
**Wren tits**, map showing distribution of, 173, 174.  
*Xenopicus albolarvatus albolarvatus*, 430.  
**Yellow-legs**, 70.  
**Yellowthroat**, Western, 140.  
*Zonotrichia coronata*, 124.  
*gambelii*, 121.  
*nuttalli*, map showing range of, 123.

## ERRATA

- Page 34. Third line of fifth paragraph, *for* of tibialis posterior *read* of flexor hallucis longus.  
Seventh line from bottom, *for* **Flexor hallucis longus** *read* **Tibialis posterior**.  
Second line from bottom, *for* **Tibialis posterior** *read* **Flexor hallucis longus**.  
Page 45. Fourth line from bottom, *for* Sierra San Pedro Martir, Nelson *read* Sierra San Pedro Martir. Nelson . . .  
Page 113. *For* *haliaetus* *read* *haliaeetus*.



